



North Sea mackerel or mackerel in the North (Sea)?

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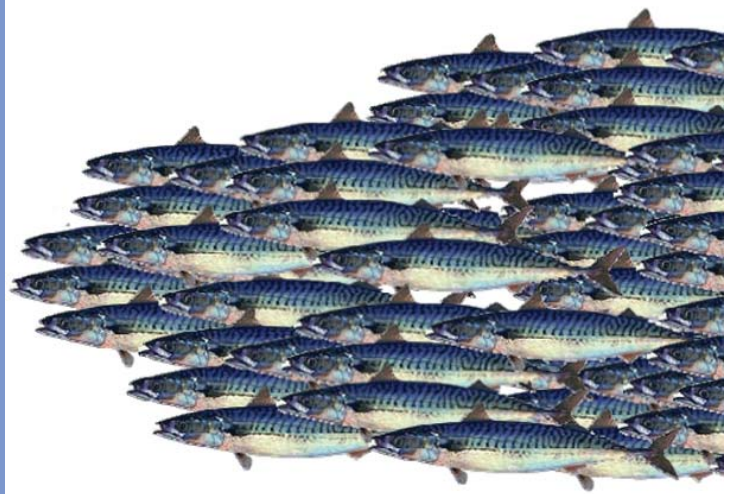
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North Sea Mackerel or Mackerel in the North (Sea)?

PhD Thesis



*"The migrations of the mackerel
have long been a subject of
speculation ..."*

Allen (1897)

Written by Teunis Scheuer Jansen
Defended 2 November 2012

North Sea Mackerel or Mackerel in the North (Sea)?

By Teunis Scheuer Jansen

PhD thesis

Colophon

North Sea Mackerel or Mackerel in the North (Sea)?

By Teunis Scheuer Jansen

PhD thesis

Defended on the 2 November 2012

DTU Aqua, National Institute of Aquatic Resources

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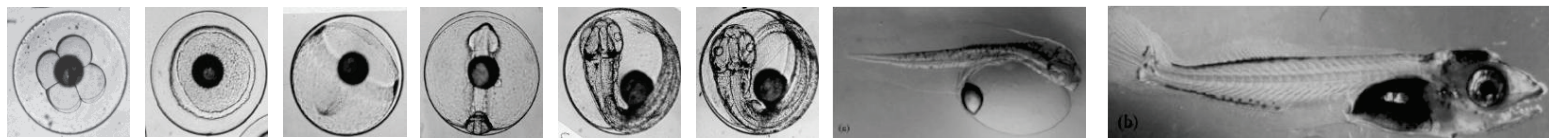
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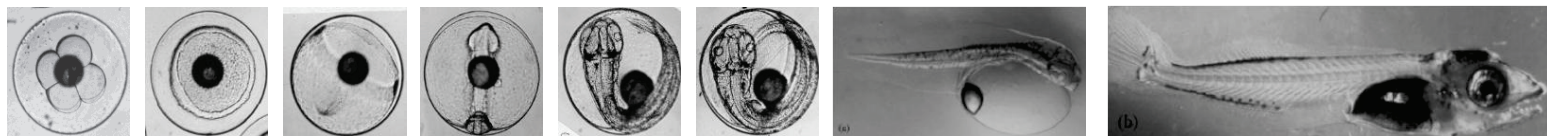
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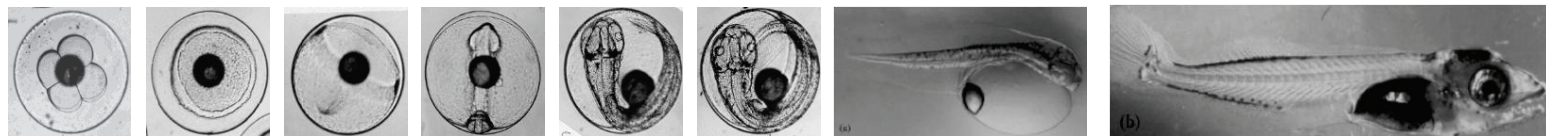
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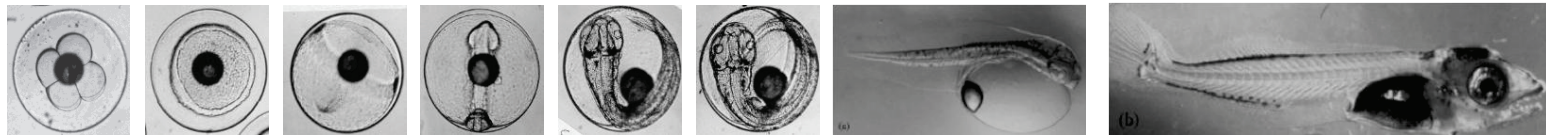
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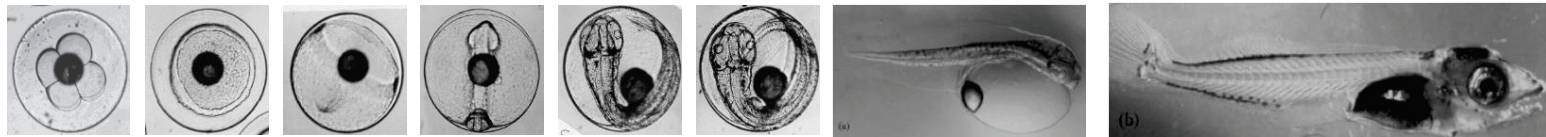


Thesis summary

Mackerel (*Scomber scombrus*) is one of the most abundant and widely distributed migratory fish species in the North Atlantic [1]. Mackerel plays an important ecological role by feeding on zooplankton and on the pelagic larval and juvenile stages of a number of commercially important fish stocks [2]. Mackerel is furthermore caught by a large pelagic fishery with annual landings between 500 and 1000 thousand tonnes [1]. Large changes in mackerel abundance and distribution have therefore significant effects on ecosystems as well as economies [2-5].

In order to predict future we must understand the past.

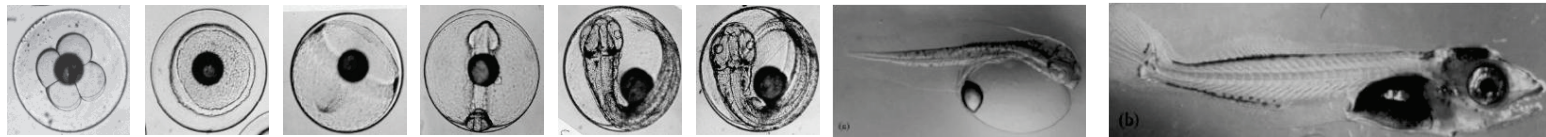
During the last century large changes in mackerel abundance and distribution have been observed in several areas of the North East Atlantic [1,6,7]. The most significant of these changes took place in the North Sea in the 1970s when the local stock collapsed [8]. 20 years later, millions of tonnes of mackerel began annual migrations into the Northern North Sea during autumn and winter [9-11]. Yet, there was no sign of recovery of the North Sea stock. Recently, mackerel dynamics in the northern parts of the distribution area have again stirred the scientific as well as the political scene [1,5,12]. The aim of this thesis is to improve the understanding of the behavioural, environmental and anthropogenic drivers behind these changes. This is done through analysis of mackerel catches from the commercial and from scientific trawl surveys, otolith analysis, age distributions and data from egg and larvae surveys. The mackerel data are combined with data on the physical environment, food availability in statistical hypothesis test, correlation analyses and state-of-art statistical models. The results



are treated in the light of a thorough review of the substantial historic literature on mackerel, and finally presented in five primary research papers and a review paper on population structure and spatial spawning dynamics of Atlantic Mackerel.

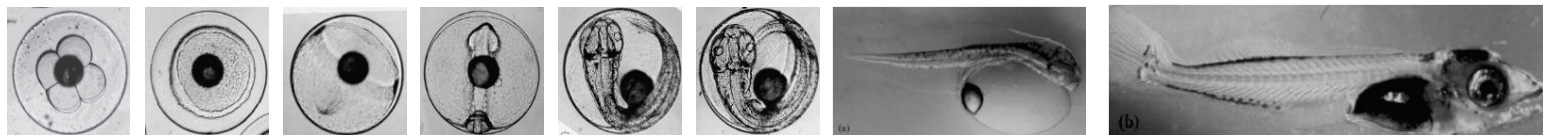
The first paper set the scene and introduces an important data set by describing the historic development of spawning in the North Sea. In “*Jansen et al. 2012. Long-term Retrospective Analysis of Mackerel Spawning in the North Sea: A New Time Series and Modeling Approach to CPR Data*” ([6], appendix I), we present a unique view of mackerel in the North Sea based on a new time series of larvae caught by the Continuous Plankton Recorder (CPR) survey from 1948-2005, covering the period both before and after the collapse of the North Sea stock. Hydrographic backtrack modelling suggested that the effect of advection is very limited between spawning and larvae capture in the CPR survey. Using a statistical technique not previously applied to CPR data, we then generated a larval index that accounts for both catchability as well as spatial and temporal autocorrelation. The resulting time series documents the significant decrease of spawning from before 1970 to recent depleted levels. Spatial distributions of the larvae, and thus the spawning area, showed a shift from early to recent decades, suggesting that the central North Sea is no longer as important as the areas further west and south. These results provided a consistent and unique perspective on the dynamics of mackerel in this region that proved invaluable in the later studies.

In order to explain the historic development of spawning in the North Sea, some key questions needed to be addressed. Is the North Sea mackerel a distinct natal homing stock or connected



to the western mackerel, may be even as a part of a large panmictic population? If the mackerel that spawn in the North Sea are isolated then the spawning is a function of recruitment, growth and mortality. However, if the North Sea population is not completely isolated from other spawning components, then the dynamics increase in complexity. A new vital question comes into play: What makes mackerel spawn within the North Sea, environmental conditions and/or some tendency for homing?

Migration behaviour and stock structure are tightly connected and overlapping. Both issues need to be approached before substantial improvements in the understanding spatiotemporal mackerel population dynamics can be reached. Before addressing these issues directly, I investigated a key underlying aspect of spawning, namely the phenology. In, "*Jansen and Gislason. 2011. **Temperature affects the timing of spawning and migration of North Sea mackerel***" ([13] , appendix II), we examined the influence of temperature on the timing of the spawning and migrations of North Sea Mackerel using data from larvae CPR surveys, egg surveys and commercial landings from Danish coastal fisheries in the North Sea, Skagerrak, Kattegat and inner Danish waters. The three independent sources of data all showed that there is a significant relationship between the timing of spawning and sea surface temperature. Large mackerel are shown to arrive at the feeding areas before and leave later than small mackerel and the sequential appearance of mackerel in each of the feeding areas studied supports the anecdotal evidence for an eastward postspawning migration. Occasional commercial catches taken in winter in the Sound N, Kattegat and Skagerrak together with catches in the first quarter IBTS survey furthermore indicated some overwintering here. Significant relationships between temperature and North Sea mackerel spawning and migration had not been

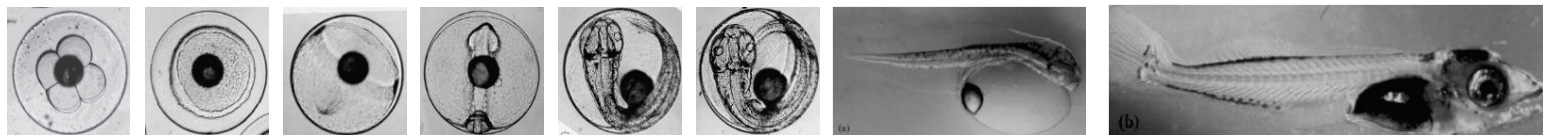


documented before.

On this basis, I could proceed to investigate the spawning migration that brings mackerel into the spawning areas in the North Sea. The first part of the spawning migration occurs from autumn through winter. In “*Jansen et al. Submitted. **Temperature, Migration and Fisheries of North East Atlantic Mackerel (*Scomber scombrus*) in Autumn and Winter***” ([7], appendix III), we investigated the spatial changes in mackerel fisheries over hundreds of kilometers that have been suggested to reflect climate-driven changes in mackerel migration patterns. However, previous studies have not been able to demonstrate this link. In this paper we showed correspondences between temperature and mackerel migration / distribution proxied by mackerel catch data from both fisheries independent bottom trawl surveys and commercial fisheries. We showed that mackerel aggregate and migrate 500 km along the continental shelf edge from mid-November to early March and that this migration follows the relatively warm shelf edge current. Variation in the timing of migration was significantly correlated to temperature changes in this current. We argued that, as a consequence of this affinity, mackerel are guided towards the main spawning areas in the south.

The validity and precision of the proposed proxies for mackerel distribution were tested by cross-comparison. We found the proxies to be significantly correlated. However, the correlations were weak and only significant in times without large changes in legislation or technical development of the fisheries. Substantial caution should therefore be exerted when using such data as proxies for mackerel distribution.

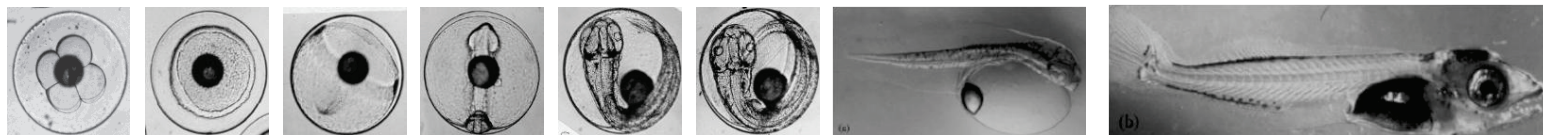
Our results included a new temperature record for the shelf edge current obtained by embedding the available hydrographic observations within a statistical model needed to



understand the migration through large parts of the life of adult mackerel and for the management of this major international fishery. The model furthermore prepared the ground for hindcasting the environmental conditions that affected the early part of the spawning migration in the decades before and after the collapse in the North Sea. This should later turn out to be an important feature for the understanding of the history of mackerel in the North Sea.

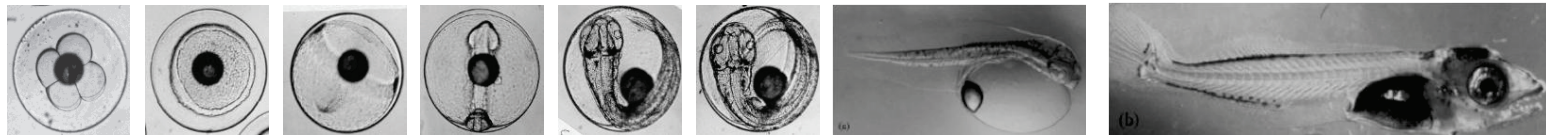
The last part of the spawning migration is tightly coupled to the stock structure issue. Knowledge of the population structure of fish species is key to understanding its basic population biology and subsequently the more complex spatiotemporal changes. The spatial population structure of mackerel has therefore been the subject of repeated studies over the last 100 years of mackerel science [14,15]. However, the pivotal behavioural concepts of homing, straying and spawning component isolation has remained unsolved. New studies and a review of old studies were therefore an imperative step towards an understanding of northern mackerel. Consequently, this was the subject for the last two primary research papers and the first part of the review paper, where a literature review supplemented with demographic data, was used to develop a conceptual model of the spawning biomass fluctuations in the North Sea.

In the paper “*Jansen et al. Submitted. **Natal homing of North Eastern Atlantic Mackerel (*Scomber scombrus*) as revealed by juvenile growth patterns***” ([16], appendix IV), we found that juvenile growth patterns indicated inter-cohort natal homing behaviour among North East Atlantic mackerel. This means that a significant proportion of a given year class will return to



spawn at higher latitudes, than other individuals from the same year class that were hatched at lower latitudes. Comparison of growth data (fish length) with latitude shows that southern juvenile mackerel attain a greater length than those further north before growth ceases during their first winter. A similar significant relationship was found between the growth in the first year (derived from the inner winter ring on otoliths) and latitudes for adult mackerel spawning between 44°N (Bay of Biscay) and 54°N (west of Ireland), a finding consistent with natal homing. No such relationship was found in mackerel spawning at more northerly latitudes, possibly as a consequence of increased spatial mixing in a more energetic regime.

The rejection of the panmictic population model left two options; if the natal homing behaviour was strong, then the spawning components may be isolated. If other factors could dominate over the tendency for natal homing, then a more intermediate, perhaps metapopulation, structure would be the case. Straying between spawning components was therefore the subject of the fifth paper *Jansen. Submitted. “Mixing Between Mackerel (*Scomber scombrus*) Stocks in the Northern Spawning Areas”* ([17], appendix V), where I rejected the former de-facto accepted hypothesis of isolated spawning components by demonstrating relationships between spawning in western and North Sea areas. My findings, based on unique larvae samples collected before the North Sea mackerel collapse, show that the exchange is not a recently emerged phenomenon due to the collapse. The key factor driving this part of the spawning migration dynamics was likely to be spring temperature, as the exchange was found to be strongly correlated with temperature in the current that flow NE along the shelf edge from West to North of Scotland where it enters the western North Sea through the Fair Isle channel and East of the Shetland Islands.



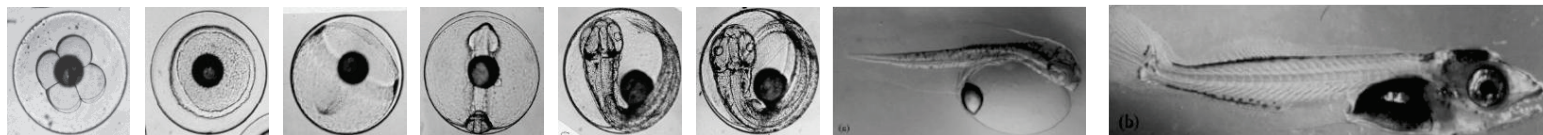
Further analysis of the interplay between homing and straying was done through a review of existing literature covering both the spawning areas in the North West and North East Atlantic, supplemented with demographic data, and used to develop a conceptual model of the spawning biomass fluctuations in the North Sea. These results were presented in

*"Jansen. In prep. **Population structure and spatial spawning dynamics of Atlantic Mackerel***

*(**Scomber scombrus**)"* ([18], appendix VI): Mackerel clearly displays isolated and different life-cycle patterns across the Atlantic Ocean. On each side, there seem to be a complex of spatiotemporal diversity, but it is not evident that they divide further into more closed life cycle patterns i.e. contingents. It appears that a dynamic interplay between natal homing and substantial straying result in a more complex structure than what is reflected in the traditional separation into spawning components. On this basis, I suggest that the mackerel population in the North East Atlantic is better described as a dynamic cline, rather than connected entities. Hydrography and mackerel behaviour may then affect the steepness of the gradient at various locations within the cline as these features vary for each generation.

The dramatic history of mackerel in the North Sea consequently needed to be reviewed by expanding the single stock assessment techniques to account for migration dynamics and exchange with other spawning areas.

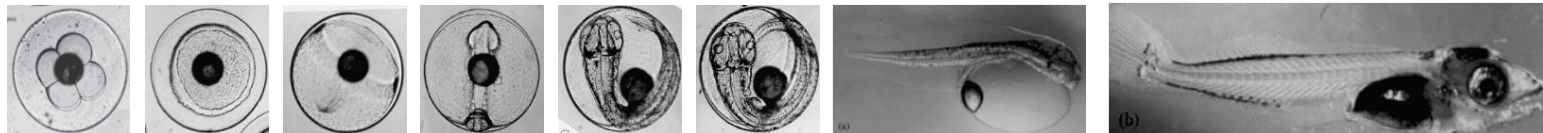
A simple outline of the novel population model of mackerel in the North East Atlantic, combined with the improved understanding of the environmental drivers of migration that were provided in the first five papers, were used to investigate the most dramatic change in the mackerel history, namely the collapse of the mackerel in the North Sea in the 1970s. I found that the traditional explanation of the collapse seems to have overlooked a range of



unfavourable environmental changes that likely added to the effect of high fishing pressure. I did not find indications for any irreversible genetic or behavioural loss caused by the collapse. The previously unexplained lack of rebuilding of spawning in the North Sea consequently seemed related to two environmental factors that have remained unfavourable, namely wind induced turbulence and zooplankton concentration. Furthermore, the large commercial autumn-winter fishery in the North Sea continues to land unknown quantities of mackerel with an affinity for spawning in the North Sea.

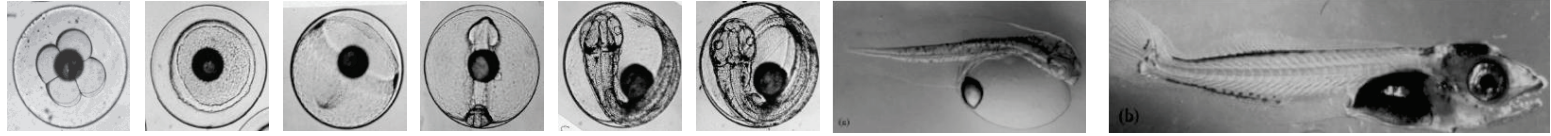
With this novel understanding, I could draw parallels between the historic development around the North Sea and the recent north-western expansion of the western spawning areas. In the North East Atlantic spawning has recently increased in the main western spawning areas and expanded into new areas towards north-west. Since the surface water in the new north-western area recently became warmer than what appeared to be critical for the historic northern spawning migration into the North Sea, it can be concluded that with regards to temperature, these areas have become favourable as a mackerel spawning habitats.

This novel interpretation of North Sea mackerel in particular and mackerel in general has implications for research, assessment and management of mackerel in the North East Atlantic and it demonstrates the dynamic spatial behaviour of a species that is purely pelagic through all its life stages. Although conservation of genetic and behavioural biodiversity should be of concern when managing mackerel fisheries, the mackerel seems less prone to unbalanced exploitation than many other commercial species.

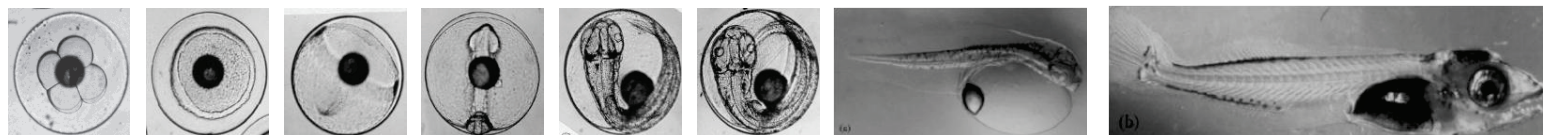


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17. Jansen T. (Submitted) Mixing Between Mackerel (*Scomber scombrus*) Stocks in the Northern Spawning Areas. PLoS One .



18. Jansen T. (In prep) Population structure and spatial spawning dynamics of Atlantic Mackerel (*Scomber scombrus*). .



Short summary / introduction

Mackerel (*Scomber scombrus*) is one of the most abundant and widely distributed migratory fish species in the North Atlantic [1]. Mackerel plays an important ecological role by feeding on zooplankton and on the pelagic larval and juvenile stages of a number of commercially important fish stocks [2]. Mackerel is furthermore caught by a large pelagic fishery with annual landings between 500 and 1000 thousand tonnes [1]. Large changes in mackerel abundance and distribution have therefore significant effects on ecosystems as well as economies [2-5].

In order to predict future we must understand the past.

During the last century large changes in its abundance and distribution have been observed in several areas of the North East Atlantic [1,6,7]. The most significant of these changes took place in the North Sea in the 1970s when the local stock collapsed. 20 years later, millions of tonnes of mackerel began annual migrations into the Northern North Sea during autumn and winter. Yet, there was no sign of recovery of the North Sea stock. Recently, mackerel dynamics in the northern parts of the distribution area have again stirred the scientific as well as the political scene [1,5,8]. The aim of this thesis is to improve the understanding of the behavioural, environmental and anthropogenic drivers behind these changes. The thesis consists of five primary research papers and a review that synthesise the red thread in the research.

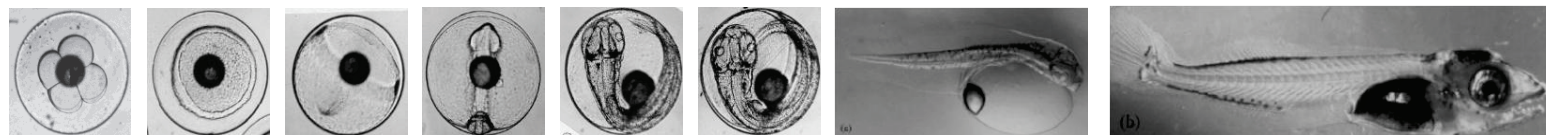
The two first describe the historic development and phenology of spawning in the North Sea:

Jansen, T., Kristensen, K., Payne, M., Edwards, M., Schrum, C., & Pitois, S. (2012). Long-term Retrospective Analysis of Mackerel Spawning in the North Sea: A New Time Series and Modeling Approach to CPR Data. PLoS One, 7(6).

Jansen, T., & Gislason, H. (2011). Temperature affects the timing of spawning and migration of North Sea mackerel. Continental Shelf Research, 31, 64-72.

The third present the analysis of spawning migration during autumn and winter:

*Jansen, T., Campbell, A., Kelly, C. J., Hátún, H., & Payne, M. (Submitted). Temperature, Migration and Fisheries of North East Atlantic Mackerel (*Scomber scombrus*) in Autumn and Winter. PLoS One.*



Knowledge of the population structure of fish species is key to understanding its basic population biology and subsequently the more complex spatiotemporal changes. New studies were an imperative step towards an understanding of northern mackerel. Consequently, this was the subject for the following two studies and the first part of the review:

Jansen, T., Brunel, T., Campbell, A., & Clausen, L. A. W. (Submitted). Natal homing of North Eastern Atlantic Mackerel (Scomber scombrus) as revealed by juvenile growth patterns. PLoS One.

Jansen, T. (Submitted). Mixing Between Mackerel (Scomber scombrus) Stocks in the Northern Spawning Areas. PLoS One.

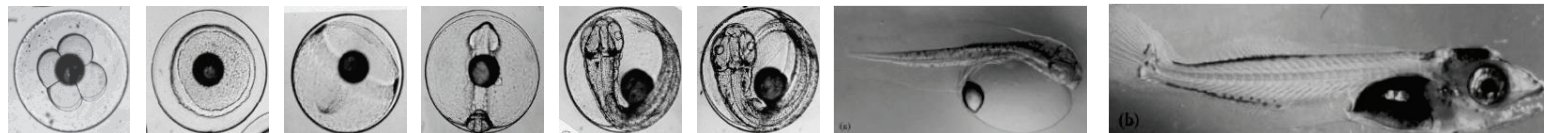
Jansen, T. (in prep). Population structure and spatial spawning dynamics of Atlantic Mackerel (Scomber scombrus).

A simple outline of the novel population model from the first part of the review, combined with the improved understanding of the environmental drivers of migration that were provided in the first five papers, was used to investigate the most dramatic change in the mackerel history, namely the collapse of the mackerel in the North Sea in the 1970s. Finally, the recent north-western expansion of the western spawning areas was reviewed in the light of the experience from the North Sea. These syntheses are described in the last part of the review paper.

Jansen, T. (in prep). Population structure and spatial spawning dynamics of Atlantic Mackerel (Scomber scombrus).

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2. Trenkel VM, Huse G, MacKenzie B, Alvarez P, Arizabalaga H, et al. (Submitted) Comparative ecology of widely-distributed pelagic fish species in the North Atlantic: implications for modelling climate and fisheries impacts. Prog Oceanogr .
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4. Cendrowicz L. (2010) The Mackerel Wars: Europe's Fish Tiff With Iceland. *Time Mag* 27. Aug.: 1-1.
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8. ICES. (2012) Ad hoc Group on Distribution and Migration of Mackerel (AGDMM). ICES CM 2012/ACOM:Xx .



Kort resume / introduktion

Makrel (*Scomber scombrus*) er en af de talrigeste og videst udbredte vandrende fiskerarter i Nordatlanten [1]. Makrel spiller en vigtig rolle i havets økosystem ved at æde dyreplankton og de tidlige livsstadier af andre økonomisk vigtige fiskebestande [2]. Dertil kommer, at makrel danner grundlag for et stort pelagisk fiskeri med årlige landinger mellem 500 og 1000 tusind tons [1]. Ændringer i makrelbestandens størrelse og udbredelse har derfor markante effekter på havets økosystem og på økonomier [2-5].

For at forudsige fremtiden må vi forstå fortiden.

I løbet af det sidste århundrede er der observeret markante ændringer i makrellens bestandsstørrelse og udbredelse i det Nordøstlige Atlanterhav [1,6,7]. De største ændringer fandt sted i Nordsøen i 1970'erne, da den lokale bestand kollapsede. 20 år senere begyndte millioner af tons af makrel at vandre ind i den Nordlige Nordsø hvert efterår og vinter. Dette var imidlertid ikke ledsaget af en genopbygning af gydende nordsømakrel. I de seneste par år har makrellen atter ført til videnskabelig og politisk røre i de nordlige egne [1,5,8]. Målet med denne afhandling er at øge forståelsen af makrellens adfærd samt forstå hvorledes miljø og mennesker har influeret på disse ændringer. Afhandlingen består af fem primære forskningsartikler og en review artikel med en samlet analyse og opsummering.

De to første beskriver den historiske udvikling og fænologi af gydning i Nordsøen:

Appendix I

Jansen, T., Kristensen, K., Payne, M., Edwards, M., Schrum, C., & Pitois, S. (2012). Long-term Retrospective Analysis of Mackerel Spawning in the North Sea: A New Time Series and Modeling Approach to CPR Data. PLoS One, 7(6).

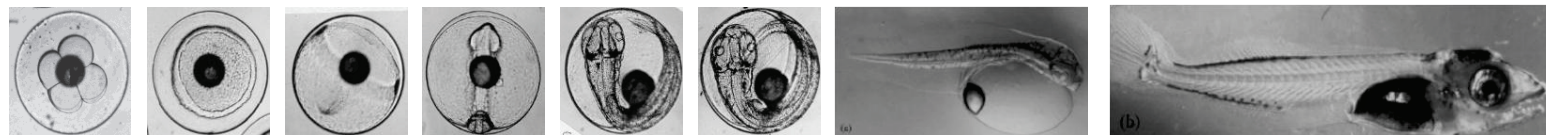
Appendix II

Jansen, T., & Gislason, H. (2011). Temperature affects the timing of spawning and migration of North Sea mackerel. Continental Shelf Research, 31, 64-72.

Den tredje præsenterer en analyse af den første del af gydevandingen (efterår-vinter):

Appendix III

*Jansen, T., Campbell, A., Kelly, C. J., Hátún, H., & Payne, M. (Submitted). Temperature, Migration and Fisheries of North East Atlantic Mackerel (*Scomber scombrus*) in Autumn and Winter. PLoS One.*



Kendskab til en vandrende fiskebestands populationsstruktur er nøglen til at forstå den mere komplekse spatiotemporale udbredelsesdynamik. Nye undersøgelser var derfor nødvendige for at øge forståelsen af makrel i de nordlige egne. Dette var målet med de følgende to artikler samt den første del af review artiklen:

Appendix IV

Jansen, T., Brunel, T., Campbell, A., & Clausen, L. A. W. (Submitted). Natal homing of North Eastern Atlantic Mackerel (Scomber scombrus) as revealed by juvenile growth patterns. PLoS One.

Appendix V

Jansen, T. (Submitted). Mixing Between Mackerel (Scomber scombrus) Stocks in the Northern Spawning Areas. PLoS One.

Appendix VI

Jansen, T. (in prep). Population structure and spatial spawning dynamics of Atlantic Mackerel (Scomber scombrus).

En simpel version af den nye populationsmodel fra den første del af review-artiklen kombineret med en øget forståelse af miljøets påvirkning fra de første fem artikler dannede grundlag for en revision af bestandskollapset i Nordsøen i 1970'erne - den mest markante hændelse i nyere makrel historik. Afslutningsvis, blev denne nye forståelse brugt til at perspektivere den nylige nordvestlige ekspansion af de vestlige gydeområder. Dette er beskrevet i den anden del af review artiklen (appendix VI).

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Appendix I

Long-Term Retrospective Analysis of Mackerel Spawning in the North Sea: A New Time Series and Modeling Approach to CPR Data

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Abstract

We present a unique view of mackerel (*Scomber scombrus*) in the North Sea based on a new time series of larvae caught by the Continuous Plankton Recorder (CPR) survey from 1948-2005, covering the period both before and after the collapse of the North Sea stock. Hydrographic backtrack modelling suggested that the effect of advection is very limited between spawning and larvae capture in the CPR survey. Using a statistical technique not previously applied to CPR data, we then generated a larval index that accounts for both catchability as well as spatial and temporal autocorrelation. The resulting time series documents the significant decrease of spawning from before 1970 to recent depleted levels. Spatial distributions of the larvae, and thus the spawning area, showed a shift from early to recent decades, suggesting that the central North Sea is no longer as important as the areas further west and south. These results provide a consistent and unique perspective on the dynamics of mackerel in this region and can potentially resolve many of the unresolved questions about this stock.

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Introduction

Mackerel (*Scomber scombrus*) is one of the most abundant and widely distributed fish species in the North East Atlantic [1]. Mackerel plays an important ecological role by feeding on zooplankton and on the pelagic larval and juvenile stages of a number of commercially important fish stocks [2]. Mackerel is furthermore caught by a large pelagic fishery with annual landings between 500 and 1000 thousand tonnes [1]. Large changes in mackerel abundance and distribution have therefore significant effects on ecosystems as well as economies. The ecological impact through altered predation pressures on secondary production and fish recruits are likely large, but currently not assessed [2]. More easily observed are the political and economic consequences [3,4].

Radical changes in abundance and distribution have been observed throughout the north-east Atlantic during the last century of developing mackerel science and fisheries [1] especially in the North Sea. The North Sea mackerel is considered to be a distinct stock that, unlike the western mackerel stock spawns inside the North Sea (Figure 1). The North Sea spawning stock was large and lightly fished up to the late 1960s, where the development of modern sonars, power blocks and single-vessel purse seining led to a ten-fold increase in mackerel landings [5]. This fishery was unsustainable and resulted in a collapse of the stock in the 1970s. Despite subsequent regulations of the fishery designed specifically

to protect this stock, it never rebuilt to its former level. In the last decade the spawning stock biomass has been 150-230 kt [1], compared to over 2 500 kt in the beginning of the 1960s [6,7]. It is currently unknown why the North Sea stock has not rebuilt to former levels.

Unfortunately, documentation of the historic development is based on fragmented information sources that do not consistently cover the whole period from before to after the collapse. This is a hindrance for addressing key questions about the lack of stock rebuilding and the consequences of these changes in distribution and abundance. An internally-consistent time-series with broad temporal span would therefore greatly aid the understanding of the development of this stock.

One such potential time series stems from the Continuous Plankton Recorder (CPR) survey in the North Sea. The CPR is a self-contained automatic plankton recorder that collects plankton continuously while being pulled by route-vessels of opportunity e.g. ferries. The monthly deployment on a variety of routes through 8 decades have resulted in a unique time series that have been a cornerstone in studies of long term-trends in the North Sea for a range of lower trophic plankton organisms [8].

Recently the analysis of fish larvae in the CPR samples has been completed up to 2005. This offer a unique opportunity to investigate long term changes in abundance and distribution of mackerel larvae.

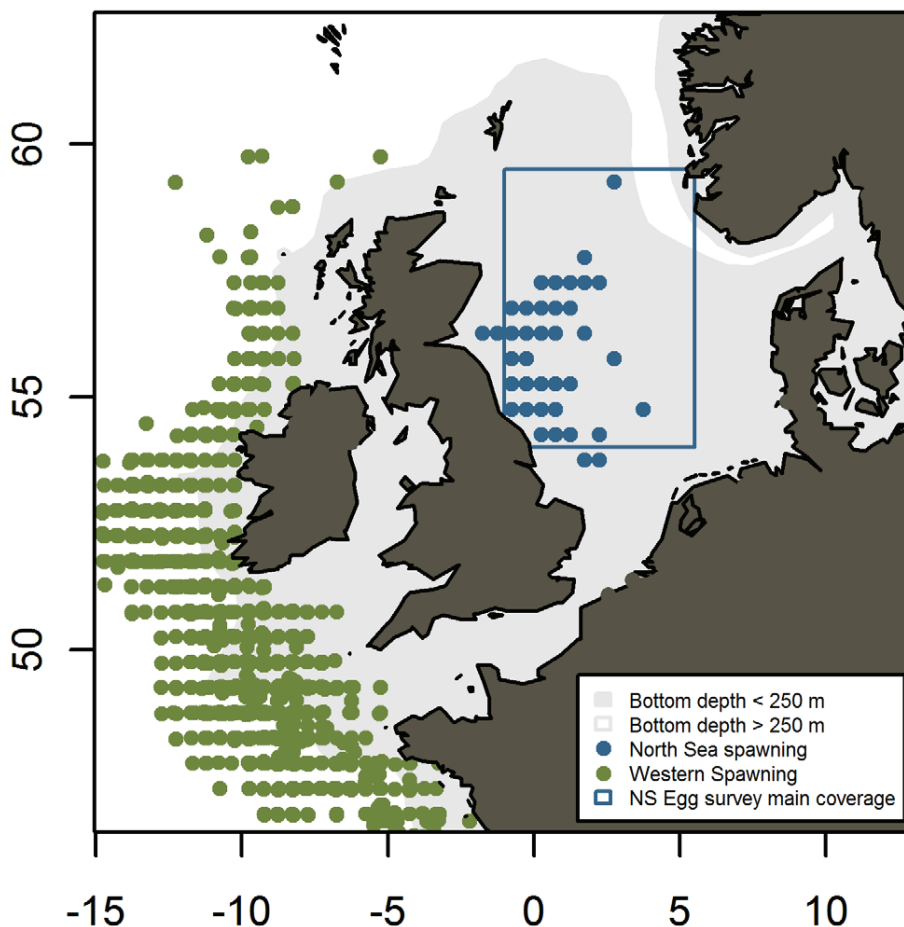


Figure 1. Mackerel populations and distribution around the north-western European shelf. Continental shelf marked in grey (bottom depth <250 m). North Sea and western mackerel spawning areas indicated by dots. Each dot marks an observation of 50+ eggs $\text{m}^{-2} \text{day}^{-1}$. Data from international mackerel egg surveys (Blue = North Sea 2002–2011 [7,34,35], Green = Western areas 1977–2007 (ICES WGMEG5)). Blue rectangle marks the approximate main coverage of the international mackerel egg survey in the latter years [7,34,35]. doi:10.1371/journal.pone.0038758.g001

We present here the new time series of mackerel abundance in the North Sea based upon larvae caught by the CPR from 1948 to 2005, spanning both the period prior to the development of the intensive fishing in the late 1960s and modern times. We verify the spatial origin of the larvae through use of a hydrographic backtracking model for all sampled larvae. Using a technique not previously applied to CPR data, we then construct a larvae index considering catchability as well as spatial and temporal autocorrelation. Considering the larvae abundance as a proxy for number of spawned eggs and spawner biomass, we compare it with existing egg survey data and fisheries-based assessments with a focus on the decline around the 1970's. We review the possible applications of this time series, including supplementing or improving the mackerel stock assessment and the international mackerel egg survey with data from the CPR survey. Finally, we provide recommendations regarding calculation procedures for CPR data.

Materials and Methods

Mackerel Larvae Data

Mackerel larvae from Continuous Plankton Recorder (CPR) surveys in 1948 to 2005 in the region 51–61°N and 3.5°W–9.5°E

were obtained from the SAHFOS database. The details of the CPR survey are described elsewhere [9,10]. Briefly, the CPR are towed by ships of opportunity at speeds in the range of 10–15 knots and at an approximate depth of 7 m [9,11]. Water enters the recorder through an aperture of 1.62 cm^2 , and is filtered through a continuously moving band of silk with an average mesh size of 270 μm . The captured plankton is fixed in formalin. The silk band is divided into samples representing 10 miles of tow for analysis, equivalent to approximately 3 m^3 of filtered seawater. Methods of counting and data processing are described by [9,10].

Thermocline Data

Thermocline depth data for the period 1948–2005 were processed from a long-term ECOSMO model run [12,13]. The model is a coupled physical-biological 3-d deterministic model. It simulates the time varying hydrodynamic and lower trophic level conditions in the region North Sea and Baltic Sea as a function of atmospheric, oceanic and terrestrial time varying boundary conditions. The thermocline data are provided on the spherical model grid (0.1° lat \times 1/6° lon) as monthly averages. Similar data from an earlier model simulation [14] are available via the ICES WGOOFE website (www.wgoofe.org) or directly from the University of Bergen (<ftp://ftp.gfi.uib.no/pub/gfi/corinna/>

WGOOFE/only_physics_run_1958_2004/ASCII/monthly/
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Effect of Larval Drift

The positions of mackerel larvae captured by the CPR survey do not necessarily correspond to the actual location where spawning took place. Ichthyoplankton can, in some regions of the North Sea, be rapidly advected away from their spawning location: the magnitude and direction of this drift can vary appreciably between years (e.g. [15,16]). As a first step in the analysis of the larval dataset, we attempted to estimate the magnitude of this advection, and thereby check for a potential bias introduced by drift processes.

As the basis for these calculations we applied an established hydrographic backtracking technique [17,18]. The backtracking calculation was performed using the IBMlib library [17], forced with hourly physical fields (currents, temperature and turbulence) derived from the NORWECOM model [19,20]. These fields were available from 1970 to 2005. Larval observations outside this period were not modelled. For each location (in time and space) where Mackerel larvae were observed in the CPR survey, 100 particles representing mackerel “larvae” were released in the model, uniformly distributed throughout the water column. Time in the model was then run backwards to determine a range of possible trajectories along which the larvae could have originated. No active-behaviour was applied to the particles – the “larvae” were mixed throughout the water column following the modelled turbulence as passive tracers. No explicit attempt was made to account for ontogenetic changes during this time (e.g. changes in egg buoyancy, hatching of eggs, changes from endogenous to exogenous feeding of larvae).

The duration of the backwards-advection scheme was based upon an estimate of time-since-spawning. Mackerel larvae in the CPR survey have a mean length of 4.8 mm (s.d. 2.0 mm) [21]. Under good temperature and food conditions, mackerel larvae grow from a typical hatch size of 3 mm to 4.8 mm in approximately 2.4 days [22]. Mackerel eggs are pelagic and therefore drift of the eggs also needs to be accounted for: typically 50% of mackerel eggs have hatched after 6.7 days at 11°C [23]. We therefore estimate that, on average, approximately 10 days have passed since the larvae captured by the CPR were spawned.

The simulated mackerel particles were therefore advected backwards in time for 10 days. At the completion of this period the geographical distance between the site of capture and the end point was calculated for each particle and the median of the distance distribution calculated. The process was then repeated for all larval observations in the CPR and the distribution of advection-distances across all observations generated. This distribution was then used to assess the magnitude and importance of advection processes in shaping the distribution of larvae.

Mackerel Larvae Model

The log gaussian cox model. The distribution of larvae captured in the CPR survey were analysed using the so-called “log-gaussian cox process” (LGCP) model [24]. This model assumes that observed larvae counts are Poisson distributed with a multivariate log-normal mean and a spatio-temporal correlation structure. Denote by i the id of the CPR sample and let N_i be the number of larvae caught in the sample. The model then states that given an unobserved/latent log-intensity in i we have:

$$N_i \sim \text{Pois}(e^{\eta_i})$$

Note that exponentiating the random variable η_i introduces overdispersion in the distribution [24] and that the latent vector η is assumed to be multivariate Gaussian.

$$\eta \sim N(\mu, \Sigma)$$

with a mean vector μ and covariance matrix Σ . The μ parameter describes the systematic effects while the covariance matrix models the random effects. Each sample unit i is associated with a set of covariates; position (cells of 0.3° latitude \times 0.6° longitude), year, day of year, thermocline depth and hour of day.

The random versus systematic effects. The spatio-temporal distribution of larvae is not completely random: aggregation in both space (“patches”) and time can be expected. Also, some degree of continuity from day to day and from year to year would be expected because the abundance of larvae are expected to be related to the stock size of the mackerel and mackerel lives and spawns for multiple years. We therefore consider the distribution of larvae as a so-called space-time separable random field with exponential correlation structure

$$\rho(\Delta x, \Delta t) = \exp(-\alpha|\Delta x|)\exp(-\beta|\Delta t|)$$

to define the covariance matrix Σ by

$$\Sigma_{ij} = \sigma^2 \rho(x_i - x_j, t_i - t_j)$$

In words this means that if we consider two samples i and j then the correlation between the two log-abundances depends in an exponentially-decaying manner on the spatial distance between the samples (Δx) and the temporal distance between the samples (Δt), where larger distances have smaller correlations. The decay of the correlation in space and time is described by the model parameters α and β . The variance parameter σ^2 describes the variations from the high abundance to low abundance areas.

In reality, even if a sample is taken in an area with high abundance, it is not guaranteed that the catch will be high. This is because individual samples from the sea generally show a high level of small scale variability. We can account for this by adding a further level of variance at the sample level. This local noise effect is also referred to as the “nugget effect” $\eta_{\text{nugget}(i)}$ [24].

It is assumed that spawning and hence larval abundance follows a fixed seasonal pattern within the year, modelled here as a gaussian. However, the yearly level is considered as a random effect:

$$\log r(y, d) = p_{\text{spawn}}(d) + \eta_{\text{spawn}}(y)$$

where $r(y, d)$ is the number of larvae on day number d in year y . The seasonal log-abundance pattern is the 2nd order polynomial $p_{\text{spawn}}(d)$. Note that a 2nd order polynomial is the logarithm of a gaussian density. The yearly log-level of the abundance is the random variable $\eta(y)$ which is assumed to be normal distributed with mean zero and variance σ^2 . A year to year correlation of this process is incorporated as exponentially decaying with the distance between years.

Due to the fact that the CPR operates horizontally in a fixed depth of approximately 7 m [9,11] the catchability (the relationship between the number of larvae present in the water column and the number of larvae caught) of the recorder can be expected to be sensitive to changes in vertical distribution of the larvae. Small mackerel larvae, such as those caught by CPR, have been observed to stay above the thermocline where they migrate towards the surface at night [25,26]. However, the water immediately behind a large, fast-moving vessel is likely to be mixed and homogenized well below the CPR towing depth [9]. To test and account for any systematic effects from changes in vertical distribution, we included diurnal migration ($\mu(h)$) and thermocline depth ($p_{thc}(thcl_i)$) in the model. Non-significant ($p > 0.05$) parameters were removed from the model. Furthermore, active avoidance of the sampling gear can also potentially affect catchability. This is more pronounced for larger larvae [26], but since the larvae caught by the CPR are small, we assumed that this effect was negligible.

Model summary. The log-intensity of individuals for sample number i taken at position x , year y , day number d , hour h is

$$\eta_i = \eta_{space \times time}(x, y) + \eta_{nugget}(i) + \eta_{spawn}(y) + p_{spawn}(d) + P_{thc}(thcl_i) + \mu(h)$$

where

- $\eta_{space \times time}(x, y)$ is a mean zero gaussian stochastic process with covariance matrix

$$(\sigma^2 \rho(x_i - x_j, y_i - y_j))_{ij}$$

- $\eta_{nugget}(i)$ is mean zero gaussian noise with variance σ_0^2 .
- $\eta_{spawn}(y)$ is a mean zero stochastic process with covariance matrix $(\sigma^2 \exp(-y|y_i - y_j|))_{ij}$.
- $p_{spawn}(d)$ is a second order polynomial ($a_{spawn1}d + a_{spawn2}d^2$) in the day number, d .
- $p_{thc}(thcl_i)$ is a second order polynomial ($a_{thcl1}thcl + a_{thcl2}thcl^2$) where $thcl_i$ is the thermocline depths at sample i .
- $\mu(h)$ is a parameter vector with one level for each hour of the day.

Fitting the model. The model was fitted as in [24] by the maximum likelihood method using the Laplace approximation. It is an important feature of the approach that it can deal consistently with missing data: latent variables (no direct observation) are integrated out of the likelihood function. Furthermore a “best guess” of any latent variable can be reconstructed based on the likelihood function. More precisely we used the conditional expectation of the variable given the data. This estimator has the property of being unbiased and having smaller variance than any other unbiased estimator [24].

The fitted model was used to predict the larvae concentration at any point in the North Sea, through each day in the period 1948–2005. From this dataset we produced yearly distribution maps and a time series of yearly indices of larvae abundance, by calculating the posterior mean of the spatially integrated intensity for each year. The hypothesis of a change in abundance from before 1970 to after 1990 was tested by a likelihood-ratio hypothesis test.

The model was run in R v.2.13.1 with the package “lge”. This package was developed in R and C and is available on request to kaskr@aqua.dtu.dk.

The annual larvae abundance index was compared to estimates of egg numbers and spawning stock size taken from the ICES WGwide reports and following publications [6,27–29].

Results

The CPR dataset consisted of 129,764 samples with 4,642 larvae observations. The samples are broadly distributed throughout the North Sea region (Figure 2a) and fairly equally distributed over the years (Figure 2b), within each year (Figure 2c) and day (Figure 2d). However, the sampling effort was poor in the central North Sea in the last decade of the time series (Figure S1).

Hydrographic drift simulations showed that advection of the larvae between the estimated spawning time and capture by the CPR was generally minor (Figure 3a). 90% of the larvae caught by the CPR had drifted less than 60 km from the spawning site and 75% have drifted less than 35 km (Figure 3b). Advection of mackerel eggs and larvae between spawning and capture in the CPR, and therefore any interannual variability associated with it, can reasonably be assumed not to induce a significant bias in the spawning distribution when looking for changes at the scale of the North Sea basin. The CPR larval observations can therefore be used as proxies for the spawning distribution of North Sea mackerel.

Larvae abundance model parameters are given in Table 1. Spatial correlation was found to be 0.65 on a 100 km distance ($\exp(-100 \cdot \alpha)$). Temporal correlation between adjacent years was estimated to be 0.74 ($\exp(-1 \cdot \beta)$). The “nugget effect” was found to be highly significant ($p < 0.001$).

Of the two catchability effects; thermocline depth was found to be significant ($p < 0.001$) whilst the diurnal catchability pattern (hour effect) was not ($p = 0.75$). Consequently only thermocline depth was retained in the final model. Catchability peaked in areas where the CPR was sampling just above the thermocline. Larvae were rarely caught when the thermocline was below 45 m (Figure 4). Having corrected for catchability effects, we assume that the CPR catches represents the true larvae concentration plus random sampling error.

The seasonal peak of the larvae abundance was found to be in mid-July (day number 193, see Figure 5). Since we estimated mean larval age to be approximately 10 days, this corresponds to a peak in spawning at the start of July. This is comparable to egg survey based estimates from 1982–2008, where the peak spawning were found to be 8–20 days earlier [30]. A difference in this direction were expected because our study period includes cooler decades than the period from 1982 to 2008 and spawning is known to be earlier in warm years [30].

Annual larvae abundance index is illustrated for the whole study period in Figure 6. We found a significant ($p < 0.001$) shift in the mean larvae index of 6.1 from before 1970 to 1.6 after 1990 (Figure 6). There is unfortunately too much variability in the CPR larval index to precisely pinpoint the onset and completion of this decline (Figure 6; Figure 7a). Nevertheless, the broad pattern of a systematic decline in abundance between 1970 and the mid-1980s shown here agrees with data from other independent sources e.g. standardized catch rates in the Dutch commercial spring fishery and catch/tagging based assessments indicate a decline beginning in the late 1960s (Figure 7b,c). The decline continues through the 1970s, as also indicated by the catch/tagging based ICES assessment and early mackerel egg surveys (Figure 7d,e), ending the decline in the mid 1980's. The CPR larval index is therefore in

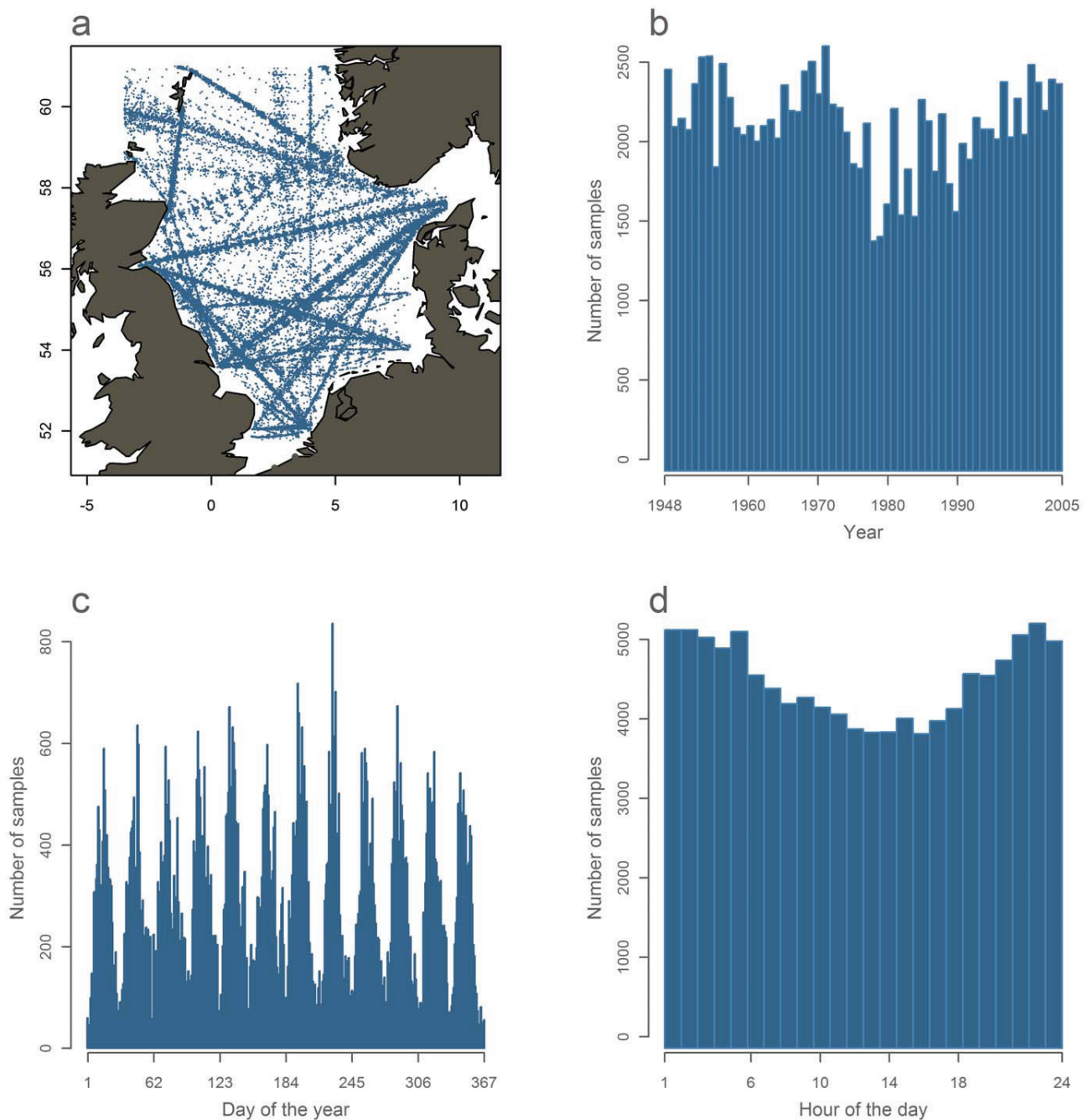


Figure 2. Continuous plankton recorder samples from 1948–2005 in the studied area. a) map of samples locations. b) number of samples by year. c) number of samples by day number of the year. d) number of samples by the hour of the day.
doi:10.1371/journal.pone.0038758.g002

broad agreement with the piecemeal picture available from other data sources: however, it also has the clear advantage of covering the entire time-span of interest.

Spatial distributions obtained from the model showed a shift in spawning area from early to recent decades (Figure 8 and S2), suggesting that the central North Sea is no longer as important as the areas further west and south. This change is in line with the results from the international mackerel egg surveys; although these surveys do not cover the extreme south and southeast (Figure 1) (ICES WGMEGS reports and pers. comm. S. Iversen, 13 Oct.

2011). Spawning in the north-western North Sea was, as also observed in the egg surveys, at a very low level in all periods.

Discussion

In this work we present a unique time series describing the dynamics of the North Sea mackerel. For the first time for this stock, a single unbroken time series, based on a consistent sampling methodology with broad spatial and temporal coverage, has been presented. The time series covers the full time span of

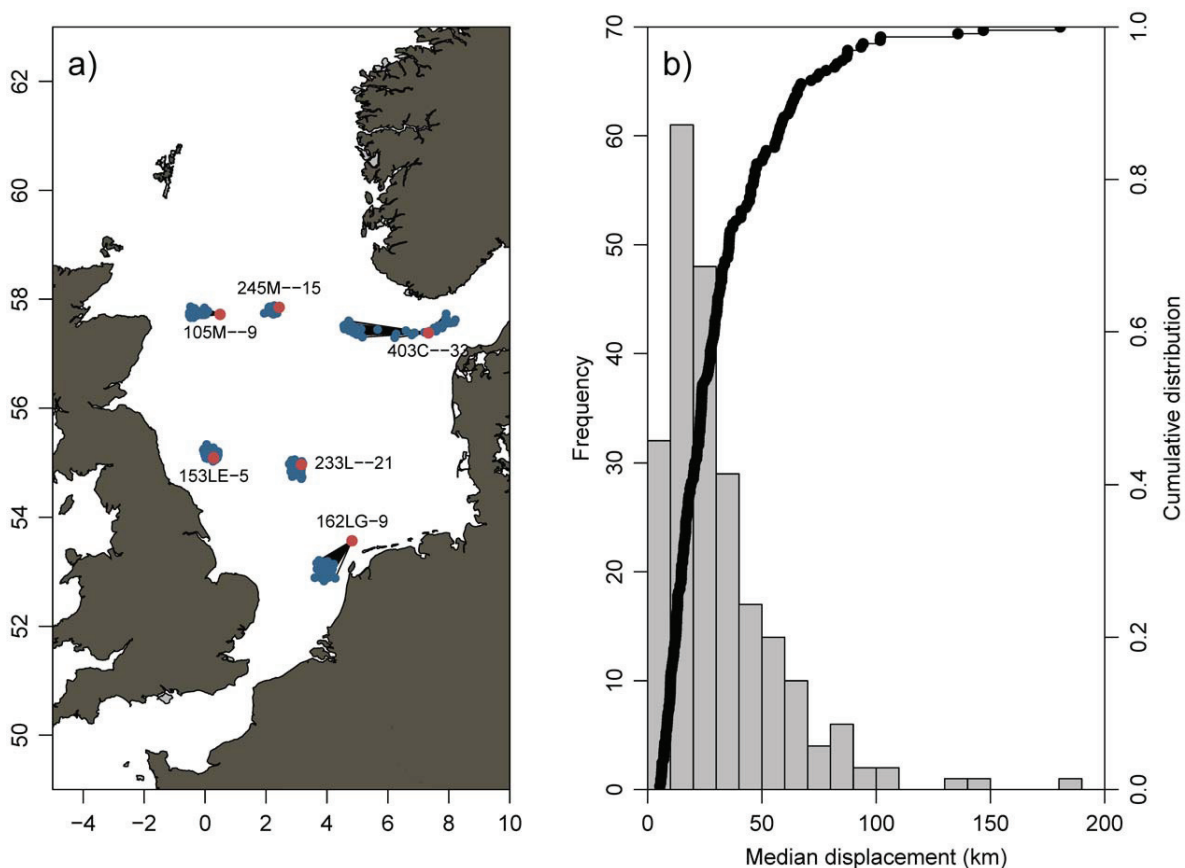


Figure 3. Backtracking simulations. a) Examples of backtracked trajectories for six observations of larval in the CPR distributed across the North Sea. Red circles mark capture points in the CPR, blue circles the end points of particles after 10 days of backtracking. Black lines connect the two points for visual reference. Text denotes the CPR label code. b) Distribution of particle displacements after 10 days drift. Left axis (grey bars) depict the frequency (number of CPR observations containing larvae) for each 10km class bin. Black-line with black dot (right axis) shows the empirical cumulative distribution function.

doi:10.1371/journal.pone.0038758.g003

interest, from 1948, through the 1970s and 1980s stock collapse, all the way up to 2005. This index is based on a novel analysis of Continuous Plankton Recorder observations, using powerful modern statistical techniques. The resulting perspective is both unique and gives a broad view of the dynamics of this population where previously only brief glimpses were available.

Our results confirmed the long-term development of the North Sea stock, previously based on assessments of spawning stock size

Table 1. Larvae model parameter estimates.

Parameter	Estimate	s.d.
σ_0^2	2.36	0.17
σ^2	6.43	2.08
$\text{Log}(\alpha)$	-5.45	0.19
$\text{Log}(\beta)$	-1.22	0.22
aspa_{w1}	2.41×10^{-1}	2.44×10^{-2}
aspa_{w1}	6.21×10^{-4}	2.77×10^{-5}
athcl1	8.33×10^{-2}	2.46×10^{-2}
athcl2	2.71×10^{-3}	7.48×10^{-4}

doi:10.1371/journal.pone.0038758.t001

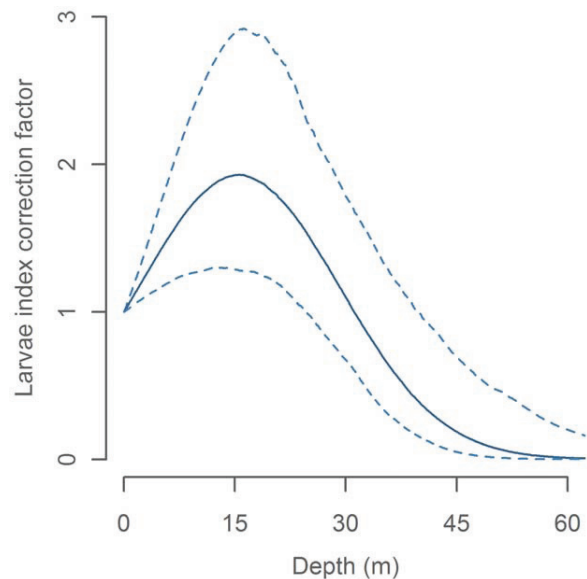


Figure 4. Catchability effect of thermocline depth on CPR larvae index.

doi:10.1371/journal.pone.0038758.g004

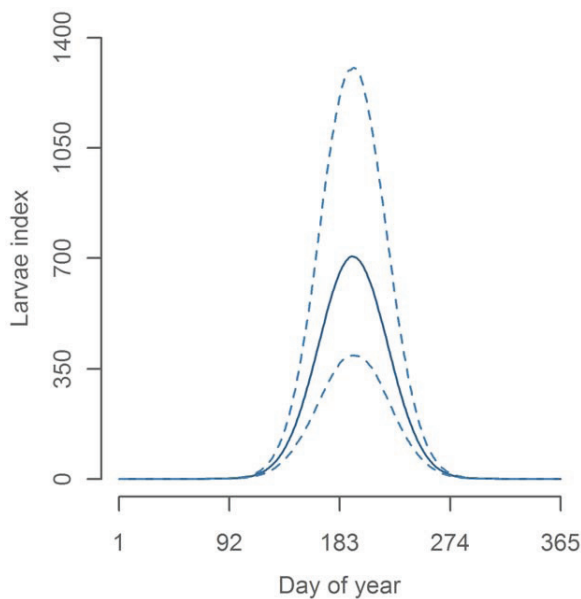


Figure 5. Seasonal effect on CPR larvae index.
doi:10.1371/journal.pone.0038758.g005

and egg abundance covering part of the time span. Furthermore we found a spatial shift corresponding to a similar observation in egg distribution. This provides some validation for all approaches and suggests that the larvae index, at least on longer time scales, is a usable proxy for egg abundance and spawning stock size in the North Sea.

It is noteworthy that the uncertainty and interannual variability in the CPR index was very high. Several sources of variability seem possible: i) high statistical uncertainty such as random sampling error that increase due to the few larvae being captured in the later years, ii) variation in fecundity, iii) variation in mortality during the approximately 7 days of egg phase and 2 days of larval phase, iv) poor spatial sampling coverage in the central North Sea in later years, v) lack of sampling in Skagerrak/Kattegat.

However, our conclusion on the decline from before 1970 to after 1990 seems robust to these uncertainties. Even though sampling intensity in the central North Sea has been reduced in the later decades, the sampling that did take place in this area did not result in catch rates comparable to those in the earlier decades. Furthermore, analysis of the spatial patterns (Figure 8) also suggests that the central North Sea is no longer as important as the areas further west and south. However, a spatial shift back towards the central North Sea in the future might not readily be detected with the present survey design. Improved spatial coverage in this region would therefore improve the precision of the CPR larval index and further increase the value of this time series for the scientific community as well as stock advice and management.

Spawning is also known to take place in Skagerrak/Kattegat. The importance of this area is possibly limited to approximately 5% of the North Sea mackerel spawning [31]. However, this estimate is highly uncertain as the area has never been properly covered by the CPR or egg survey.

The CPR survey covered parts of the North Sea outside the egg survey area, providing an opportunity to evaluate the spatial coverage of the North Sea egg survey (Figure 1 and 8). Modelled distribution of larvae in the whole North Sea showed that the Southern North Sea has been a relatively important spawning area in the North Sea through the last decades. This result suggests that

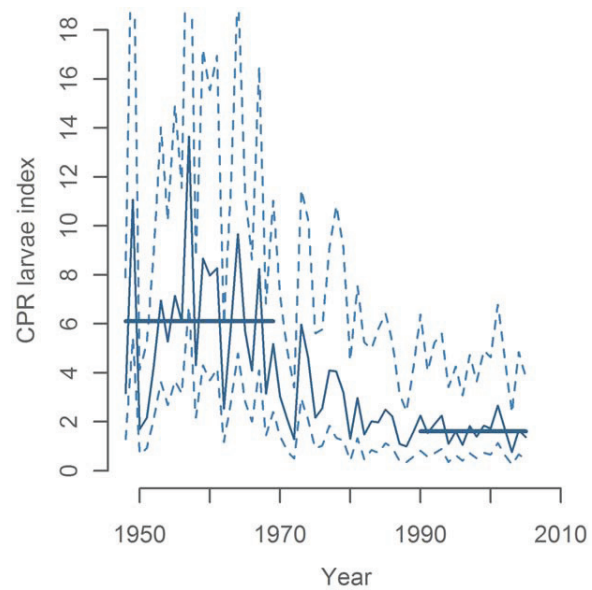


Figure 6. Larvae abundance index with 95% confidence interval.
doi:10.1371/journal.pone.0038758.g006

the area covered by the mackerel egg survey does not cover the entire spawning distribution, and may need to be expanded.

The described incomplete spatial coverage of both egg and larvae surveys, combined with the relatively high signal-to-noise ratio in the latter decades of low stock size, prevents us from validating the low level variation in SSB in the latter decades as suggested by the egg survey data (figure 7f).

The new time series developed herein has the potential to address several outstanding problems regarding the mackerel stock in the North Sea. The most significant of these is: “Why has the North Sea spawning stock not rebuilt despite decades of protection from commercial fisheries?”. We propose four hypothesis that may explain this observation: i) Changes in environment or predation pressure have reduced the productivity of the stock; ii) The fishing pressure is still too high due to by-catches in herring fisheries and/or in the large fishery for western mackerel in the northern North Sea; iii) The North Sea mackerel is not a separate natal homing stock and the observed collapse was merely a change in distribution of a single large north eastern Atlantic panmictic mackerel population; or iv) The North Sea mackerel was a separate natal homing stock up to the collapse where after modification of the genotype and behaviour happened as a result of intermixture between the small North Sea stock and the larger western stock [32]. Whilst it was not possible to address these questions directly here, further analysis of the CPR larval index have made a valuable contribution to testing hypothesis 3 by comparing the large interannual fluctuations with similar fluctuations in the western spawning area [33]. Furthermore, time series analysis relating the presented index with environmental factors has given indications on causal relationships between biological/physical drivers and migration [33].

Finally, phyto-, zoo- and ichthyoplankton data from the CPR survey have repeatedly been used by scientists because of the unique spatiotemporal coverage over the last 8 decades. Typical methods for compiling time series have been deterministic algorithms raising the organism count in the samples to monthly averages in designated spatial rectangles, that are then aggregated over months or rectangles to provide time series or maps [8].

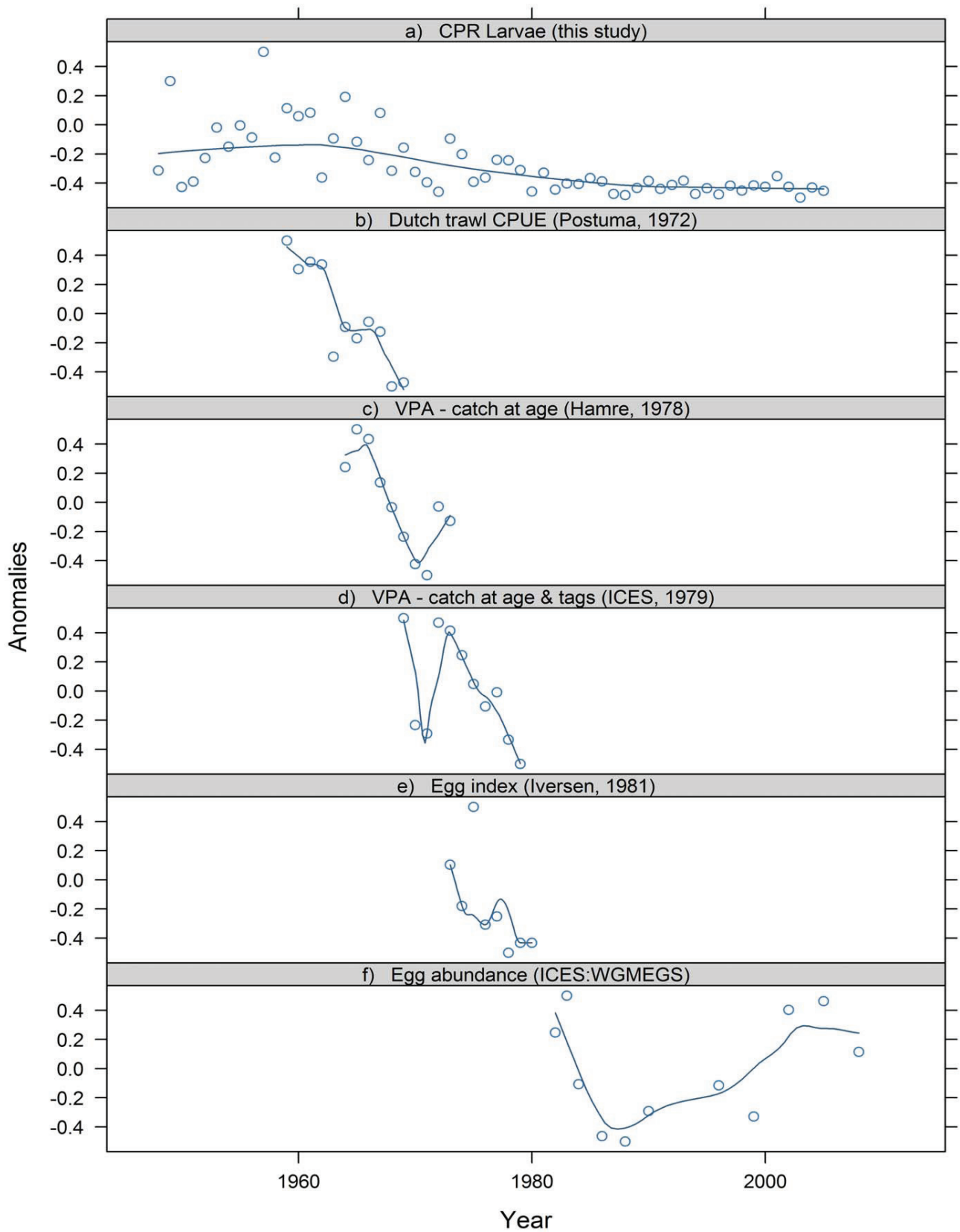


Figure 7. Long term mackerel trends in the North Sea [6,27–29]. Loess smoothed trend lines with span = 0.5.

doi:10.1371/journal.pone.0038758.g007

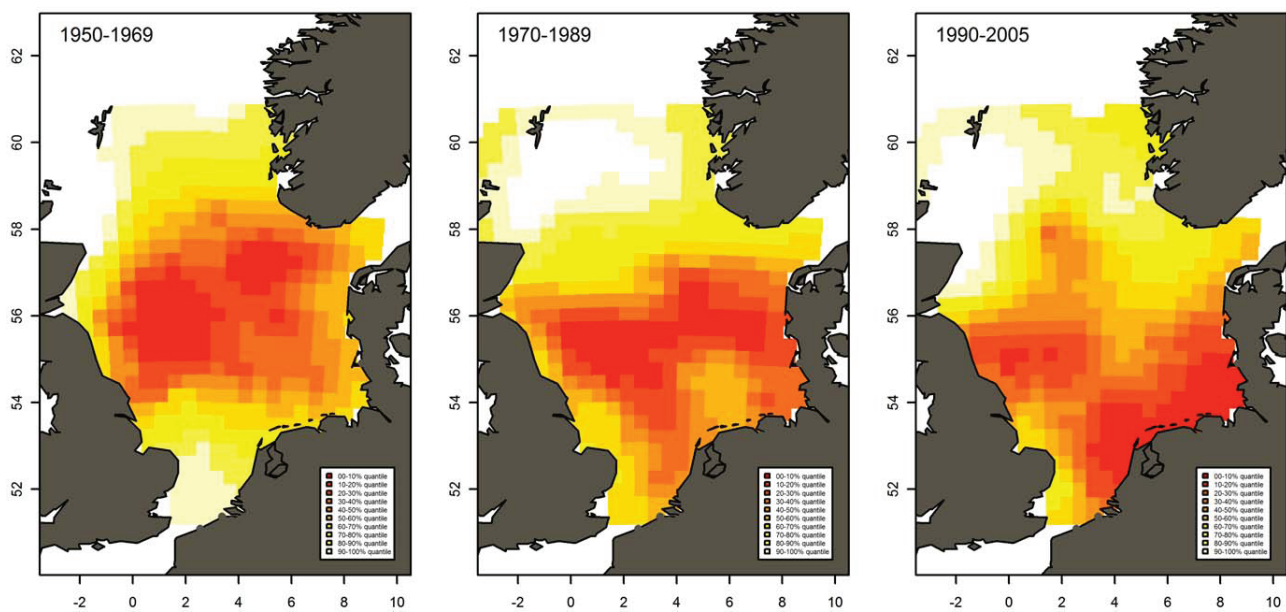


Figure 8. Modeled spatial distribution of mackerel larvae caught by CPR. Color scale from white (low abundance) represents values in 0–10% quantile, etc. up to red 90–100% quantile (high abundance).
doi:10.1371/journal.pone.0038758.g008

Present day's improvement in computer power has made it possible to apply advanced statistical models to large high resolution datasets, such as CPR plankton samples. Applying state-of-the-art statistical models such as the present log-gaussian cox process model provides numerous advantages over the more simple deterministic raising algorithms. Organisms as well as the CPR samples are often patchily distributed in time and space. Any analysis of CPR data should consistently deal with these challenges, estimate the uncertainty that stem from these sources and propagate it into the final result. To deal with vertical patchiness and migration, that can have great effect on the variance of the relation between densities in CPR samples at 7 m and the whole water column [9,11], we considered two factors with potential to affect vertical distribution. By means of hypothesis testing, we could build the final model using only the significant parameter. The horizontal distribution issues were considered by using the exact sample positions (midpoints) and accounting for the spatial correlations between samples. This allowed for a more informed estimation of larvae densities in unsampled areas what could have been obtained through simple interpolations. Furthermore, it added to the uncertainty estimation procedure. Similarly, we could model temporal autocorrelation with i) a year-to-year correlation and ii) a seasonal day-to-day correlation. All model features were accounted for when maximizing likelihood of the model-observation fit. With this model we were able to provide the most likely estimate of larval density at any position and at any time – sampled or unsampled and present maps and time series in any resolution accompanied with uncertainty estimates.

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We recommend the usage of such models for analyses of CPR data and encourage revisiting previously published studies with the aim of expansion and improvement.

Supporting Information

Figure S1 Maps of continuous plankton recorder sample locations in the spawning season May–July. a) 1948–1959. b) 1960–1974. c) 1975–1989. d) 1990–2005. (TIF)

Figure S2 Animation of modeled annual spatial distribution of mackerel larvae caught by CPR. Color scale from white (low abundance) to red (high abundance). (SWF)

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Author Contributions

Conceived and designed the experiments: TJ. Analyzed the data: TJ KK MP. Contributed reagents/materials/analysis tools: TJ KK MP. Wrote the paper: TJ KK MP. Project leader on the reanalysis of CPR samples: SP Lead lab-team reanalysing the CPR samples: ME Modelled the thermocline dataset: CS.

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Appendix II



Research papers

Temperature affects the timing of spawning and migration of North Sea mackerel

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ABSTRACT

Climate change accentuates the need for knowing how temperature impacts the life history and productivity of economically and ecologically important species of fish. We examine the influence of temperature on the timing of the spawning and migrations of North Sea Mackerel using data from larvae CPR surveys, egg surveys and commercial landings from Danish coastal fisheries in the North Sea, Skagerrak, Kattegat and inner Danish waters. The three independent sources of data all show that there is a significant relationship between the timing of spawning and sea surface temperature. Large mackerel are shown to arrive at the feeding areas before and leave later than small mackerel and the sequential appearance of mackerel in each of the feeding areas studied supports the anecdotal evidence for an eastward post-spawning migration. Occasional commercial catches taken in winter in the Sound N, Kattegat and Skagerrak together with catches in the first quarter IBTS survey furthermore indicate some overwintering here. Significant relationships between temperature and North Sea mackerel spawning and migration have not been documented before. The results have implications for mackerel resource management and monitoring. An increase in temperature is likely to affect the timing and magnitude of the growth, recruitment and migration of North Sea mackerel with subsequent impacts on its sustainable exploitation.

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1. Introduction

The change in global climate and the wish to manage fisheries sustainably have stressed the need for understanding how temperature affects the life history of important fish species (Graham and Harrod, 2009). Mackerel (*Scomber scombrus*) is an abundant migratory pelagic fish in the north-east Atlantic where it plays an important ecological role by feeding on zooplankton and on the pelagic larval and juvenile stages of a number of commercially important fish stocks (ICES, 2008). Mackerel is furthermore caught by a large pelagic fishery with annual landings between 500 and 1000 thousand tonnes. It is therefore important to understand how changes in temperature may affect its life history characteristics, including the timing of its spawning and migrations.

The mackerel in the eastern Atlantic has traditionally been divided into three spawning components named according to their spawning areas: Southern (Gibraltar to southern Biscay), Western (Biscay to northwest of Scotland), and North Sea. The North Sea component is considered to be a distinct stock (ICES, 1999). Individuals tagged during summer in Skagerrak, Kattegat, the inner Danish waters, and off north-eastern England have been recaptured in Skagerrak and the northern part of the North Sea in

October–December (Agger, 1970a, b; Lindquist and Hannerz, 1974; Postuma, 1965; Revheim, 1954, 1955). These recaptures and information from the Dutch trawl and Norwegian purse seine fisheries suggest that North Sea mackerel overwinters in the deeper parts of the Skagerrak and north-eastern North Sea from where it ascends to the surface layer in spring (Hamre, 1978; Postuma, 1965). Little information exists on its geographical distribution in the period between overwintering and spawning. The main spawning period is mid-May to late June. Spawning takes place in the central North Sea and to a lesser degree also in Skagerrak–Kattegat (ICES, 2009a; Lindquist and Hannerz, 1974). After spawning mackerel redistributes in the North Sea or migrates into nearby waters such as the Skagerrak, Kattegat, the Sound, the Belt Sea and the western Baltic Sea. Mackerel of the western and southern spawning components also enter the North Sea and Norwegian Sea (Uriarte et al., 2001; Zijlstra and Postuma, 1966) where they mix with the North Sea stock. The extend of this mixing cannot be quantified at present due to a lack of methods for assigning individual mackerel to spawning components (Jansen et al., 2009).

Over the last decades the entire north-east Atlantic stock of mackerel has been exposed to increasing temperatures (Hughes et al., 2009) and in some areas this could have affected their spawning season and migrations. The timing of the spawning of the southern and western spawning components show interannual variations, but these variations seem not to be related to temperature (Punzon and Villamor, 2009). In the mid 1990s the location of

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mackerel in the Northern North Sea was constrained by temperature before the onset of migration towards the wintering and spawning areas (Reid et al., 2001) and temperature also influenced the migration path and speed (Reid et al., 1997; Walsh et al., 1995). Data from commercial fisheries show large interdecadal changes in the timing of this migration, but again no simple correlation with water temperature seems to exist (Reid et al., 2003a, 2006; Walsh and Martin, 1986).

On the western side of the Atlantic the 7 °C isotherm was long seen as forming a temperature barrier to the northern advance of mackerel along the US east coast (Bigelow and Schroeder, 1953; Goode, 1884; Sete, 1950). Captive mackerel increase their swimming speed in water below 7 °C and this was interpreted as a behavioural response to low temperature (Olla et al., 1975, 1976). Field observations have shown that mackerel from the southern component of the West Atlantic stock avoids water below 5 °C and that most individuals are found in waters warmer than 6 °C. Furthermore, the spring distribution seems to be more northern and in-shore in warmer years (Overholtz et al., 1991). However, in 1990 mackerel from the northern component migrated into Cabot Strait where the water temperature was approx. 4 °C in order to reach their spawning grounds (D'Amours and Castonguay, 1992). D'Amours and Castonguay argued that this demonstrated how thermal preferences can become subordinate to reproductive requirements, a point supported by the fact that this stock always enter the Cabot Strait around the same date (Anon, 1896; Castonguay and Beaulieu, 1993). Few have studied the effects of temperature on the post-spawning feeding migration. However, in a study of small-scale distribution (Castonguay et al., 1992) found that increased mackerel abundance coincided with wind-induced warming of coastal water on a time-scale of days.

We investigate the impact of temperature on the timing of spawning and migration of North Sea mackerel using data from larval and egg surveys and from commercial landings. We focus on the relationship between temperature and the timing of spawning, the post-spawning feeding migration and the return migration towards the overwintering areas for different sizes of mackerel.

2. Materials and methods

2.1. Temperature data and analysis

Sea surface temperature (SST) from satellite measurements in 1982–2008 was downloaded as monthly averages from the NOAA website (<http://www.cdc.noaa.gov/>) using the dataset "NOAA_OI_SST_V2" provided by NOAA/OAR/ESRL PSD, Boulder, Colorado, USA. Average temperatures were calculated for 3 areas (North Sea, Skagerrak and Kattegat, see Fig. 1) and 10 periods: winter (December–February), pre-spawning (March–April), beginning and peak spawning (May–June), peak spawning (June), late spawning (July), post-spawning (August) and autumn (September–November). Another set of surface temperature data covering the time period from 1948 to 1977 was assembled based on temperature recordings from CTD, bottle samples, underway/pump and mooring data at depths < 10 m. The dataset was downloaded from the ICES data centre (<http://www.ices.dk/ocean/data/surface/surface.htm>) and used to calculate the average sea surface temperature in the beginning and peak spawning (May–June) and peak spawning (June) periods in the North Sea. An example of the temperature data is given in Fig. 2.

To examine the relationship between SST and temperature at the depth at which mackerel is likely to spawn a temperature dataset consisting of vertical temperature profiles from CTD and bottle samples was compiled. The data were downloaded from the ICES data centre (<http://www.ices.dk/ocean/asp/HydChem/HydChem.aspx>) and used



Fig. 1. Areas used for calculating average sea surface temperature.

to calculate average temperatures in May and June in the depth ranges 0–10, 3–20 and 20–40 m. Sufficient vertical temperature data were only available in the period from 1983 to 2008. In the North Sea mackerel eggs are distributed in the upper part of the water column and more than 90% of the eggs are found in the upper 12–13 m (Iversen, 1977). However, spawning probably occurs close to the thermocline from where the positively buoyant eggs subsequently float upwards (Coombs et al., 2001; De Lafontaine and Gascon, 1989; Myrberget, 1965; Nilsson, 1914). The ICES CTD data show that in most years a thermocline is present in the North Sea in May at depths of between 10 and 40 m while in June a thermocline is always present at 15–30 m. To examine the relationship between SST and the temperature at the depths where mackerel are likely to spawn we tested whether there was a significant positive correlation between North Sea SST and the temperature at 3–20 and 20–40 m of depth in May and June.

2.2. Landings data and analyses

Landings of mackerel from 1987 to 2008 were extracted from Danish landing records and grouped into 8 areas based on the location of the port of landing (see Fig. 3). To assure that the landings did not represent overwintering mackerel, only landings from April to November were included. Landings from vessels larger than 10 m in length or from vessels using trawl or purse seine were excluded because these vessels potentially could have operated off-shore and far from the port of landing. The resulting dataset consisted of landings from mixed fisheries mainly using passive gears such as fixed pound nets and gillnets and contained

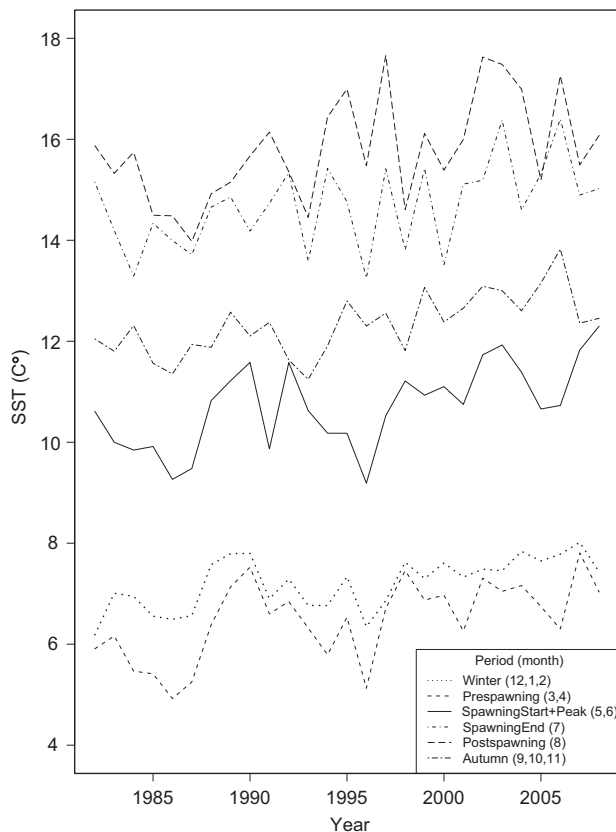


Fig. 2. NOAA temperature datasets for the North Sea.

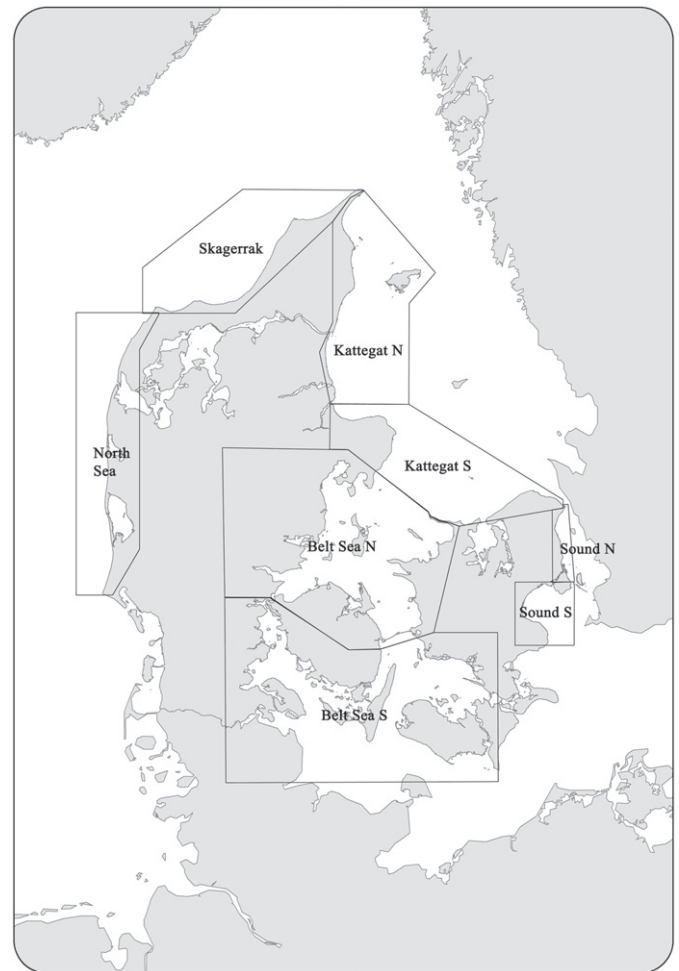


Fig. 3. Areas used for analysing the landings data.

46,442 separate landing records corresponding to a total landed weight of 6302 tons. Landings of other species from these fisheries in early spring and summer show that they were operating well before mackerel started to appear in the landings. As indicators of the arrival and departure timing of mackerel in a given area, the 10% and 90% percentiles of the cumulative catch of mackerel were used.

Landed mackerel are either sold by size category or as unsorted. Size categories are: 1 (0.5 kg and up), 2 (0.2–0.5 kg) and 3 (up to 0.2 kg). Using the landing records it was possible to analyse size dependent differences in the timing of the migration for the North Sea, Skagerrak, and Kattegat N and S, but too few mackerel were landed in size category 3 in the remaining areas to allow an analysis, perhaps as a result of discarding or because the landings were registered as unsorted. Examples of cumulative catch curves are given in Fig. 4.

The migration path and differences in arrival/departure time between areas were analysed separately for small and large mackerel in the four areas where data permitted this. In the remaining four areas landings were aggregated for all sizes. To analyse the correlation between SST and timing each of the three temperature areas in each of the five periods were related to time of arrival (departure) in the eight landing areas. We tested if the observed number of significant correlations differed significantly from the expected number of type 1 errors (detecting significant relationships where none exists) in N tests with a significance level α of 0.05. The probability equals the probability of getting the observed or more out of N binomial trials, each with a $\alpha/2$ probability of false significance for negative correlations (and $\alpha/2$ probability of false significance for positive correlations). Results where the probability exceeded 0.05 were discarded.

2.3. Larvae data and analysis

Mackerel larvae (larvae and post-larvae) obtained from Continuous Plankton Recorder (CPR) surveys from 1948 to 1977 was

kindly provided by the Sir Alister Hardy Foundation for Ocean Science (Johns, 2010; Reid et al., 2003b; Richardson et al., 2006). Survey routes sampled over a limited number of years or with very few mackerel observed were excluded, leaving route K. L and C with 1949 mackerel larvae caught in the North Sea area (53°N–60°N, 2°W–8°E) to be analysed (see Figs. 5 and 6). From this dataset only years with more than 25 larvae were used. Each route was sampled monthly through a 1.27 cm² aperture. Mackerel larvae were counted and the results expressed as the average number of larvae for each 10 nm of towing. The mean density (larvae/m³) and mean Julian day of sampling by year and month was calculated and used to estimate the Julian day (J_Q) where the cumulative density reached the quantile Q by linear interpolation between the two surrounding data points. Q_{10} and Q_{50} were used as proxies for the beginning and the peak of spawning, respectively. A simple linear model of J_Q as a function of SST was modified by adding a term to account for temperature dependent development from spawned egg to catchable larvae. The eggs hatch approximately 18 h earlier for each 1 °C increase in temperature (Mendiola et al., 2006). After hatching at approximately 3 mm the larvae grow to 4.8 mm (the mean size of larvae in the CPR samples (Coombs et al., 2001)) approximately 21 h faster for each 1 °C increase in temperature (Bartsch, 2002). For this reason the following model was applied to test whether J_Q was significantly correlated to SST.

$$J_{Q, \text{Year}} = b_0 + b_1 \text{SST}_{\text{Year}} - \left(\frac{18+21}{24} (\text{SST}_{\text{Year}} - \text{SST}_{\text{minimum in timeseries}}) \right)$$

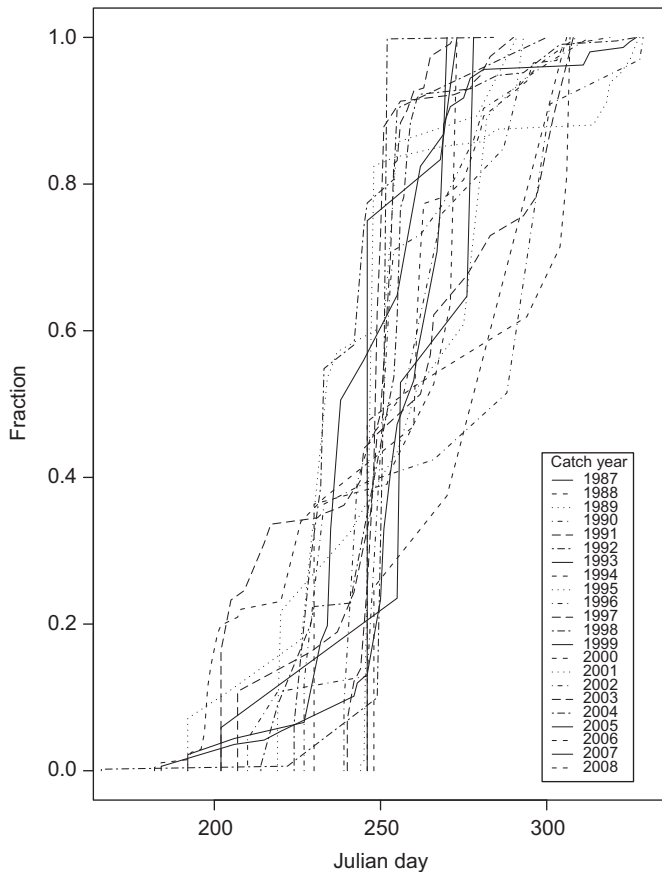


Fig. 4. Cumulative catch curves for the Sound N. Julian day on X-axis.

The proxy for beginning of spawning, J_{10} , was related to SST at beginning and peak spawning (May–June) in the North Sea, while J_{50} was related to SST at peak spawning (June).

2.4. Egg data and analysis

Mackerel egg production estimates (E) based on stage I eggs (max 24 h old) from egg surveys in 1968–2008 was used as published by ICES and others (ICES, 1997, 2000, 2003, 2006, 2009a; Iversen, 1981, 1982; Iversen et al., 1985, 1987, 1989, 1991; Iversen and Eltink, 1983; Iversen and Westgård, 1984). Only data from years with a minimum of 3 survey periods were used. From the survey with the highest E plus the two adjacent surveys before and after; the timing of peak spawning (P) was estimated as a mean of the mid-Julian day of the three surveys weighted with their respective E . In two years the last survey measured the highest E , in these cases P was set to the mid-date of the last survey. P was tested for significant correlation with SST at peak spawning time (June) in the North Sea.

For all time series the correlation analysis was adjusted for autocorrelation if the latter exceeded the 95% confidence limits of white noise ($\pm 2\sqrt{1/N}$) (Madsen, 1998). Adjustments were done by substituting the degrees of freedom with the effective number of degrees of freedom (Pyper and Peterman, 1998). All data analysis was performed in R version 2.8.1 (Ihaka and Gentleman, 1996).

3. Results

3.1. Correlation of temperature at different depths

The average temperature in the 3–20 m and 20–40 m depth intervals were significantly positively correlated to temperature in

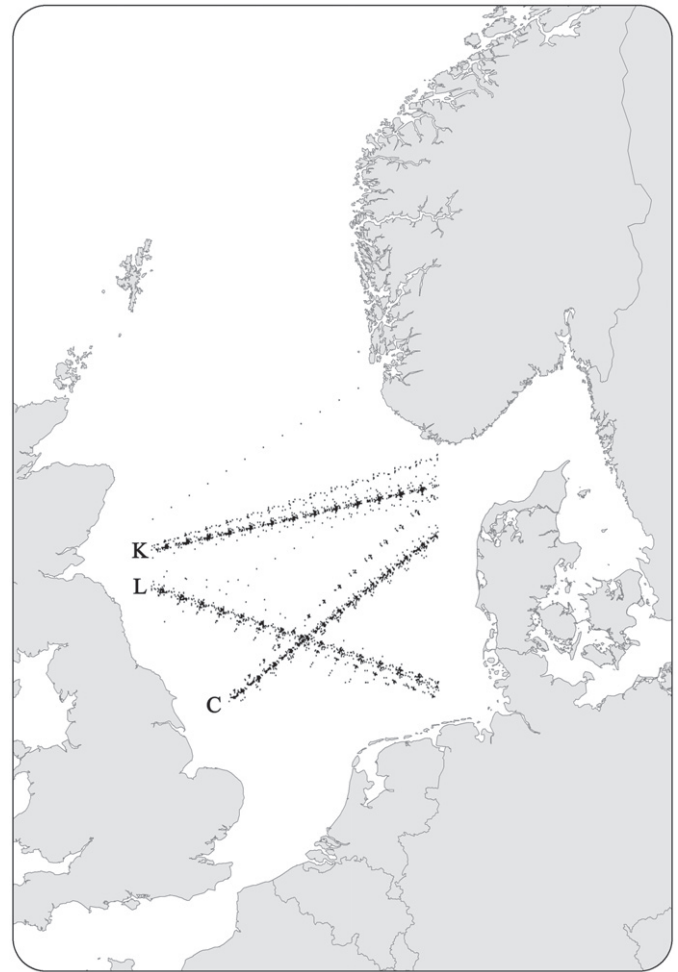


Fig. 5. Samples from the whole time series showing the three CPR routes.

the 0–10 m interval and to the satellite SST data. P values are given in Table 1.

3.2. Timing of migration

The arrival time of mackerel in the different areas matched the expected south-eastern migration (Fig. 7). The difference in arrival time between North Sea/Kattegat N/Skagerrak and the Sound/Belt Sea was highly significant (t -test; H_0 : Equal means; $n=65$; $p < 0.001$) and quite large (67 days). On average mackerel arrived 27 days earlier in the Belt Sea N than in the Sound N (t -test; H_0 : Equal means; $n=20$; $p < 0.007$). No significant differences in departure time between the different areas were observed (t -test; H_0 : Equal means; $n=65$; $p=0.085$).

3.3. Size dependency

The timing of small (< 0.2 kg) and large (> 0.2 kg) mackerel were compared in Kattegat and Skagerrak. The null-hypotheses of small mackerel arriving simultaneously with large were rejected (ANOVA; factors=area and size; $n=113$; $p < 0.001$) and so was the hypothesis of small departing simultaneously (ANOVA; factors=area and size; $n=113$; $p < 0.001$). The large fish thus arrived earlier and left later than the small. On average the large mackerel arrived 18 days before and departed 20 days after the small individuals. This lead to a significant difference of 38 days in the

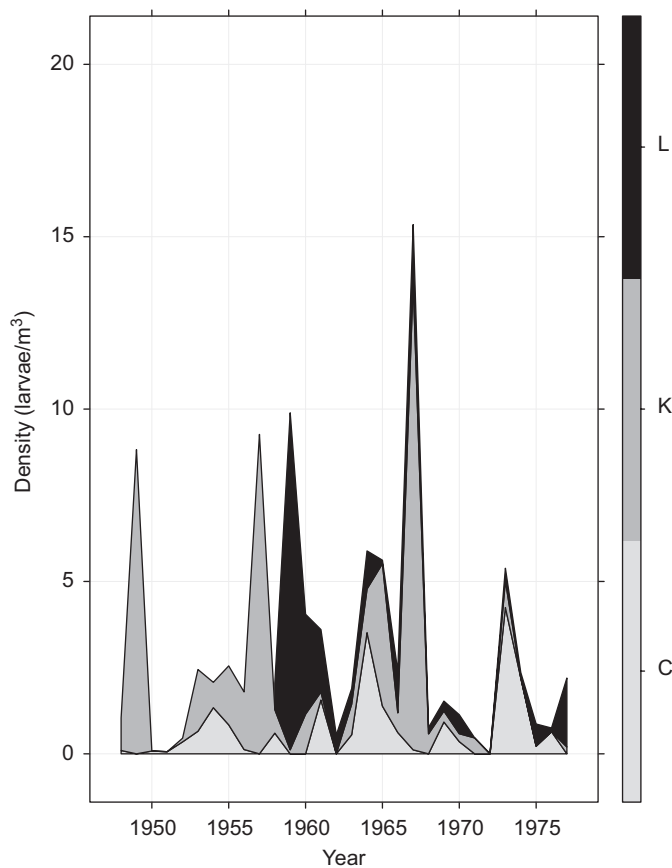


Fig. 6. Time series of the mean density (larvae/m³) in May–August by route (C, K and L).

Table 1
Relations between sea surface temperature and the temperature at the depth of spawning and egg development.

	SST _{0 m} (NOAA)	T _{3–20 m} (ICES)	T _{20–40 m} (ICES)
<i>May</i>			
SST _{0–10 m} (ICES)	< 0.001	< 0.001	0.002
SST _{0 m} (NOAA)		< 0.001	0.036
<i>June</i>			
SST _{0–10 m} (ICES)	< 0.001	< 0.001	0.001
SST _{0 m} (NOAA)		< 0.001	0.015

duration of presence (ANOVA; factors=area and size; $n=113$; $p < 0.001$). No significant difference was found in the North Sea.

3.4. Temperature dependent migration

The significant relationships between arrival time and temperature were all negative, i.e. mackerel arrive earlier in years with warmer water (Table 1). The three cases considering North Sea SST at beginning and peak spawning are shown in Fig. 8. The mean estimated effect of SST (95% confidence interval) in these cases was: -15.6 ± 12.1 days/°C (Table 2).

3.5. Temperature dependent larvae occurrence

The timing of the beginning of larval occurrence was significantly correlated with SST ($R^2=0.41$, $p < 0.003$) and so was the peak ($R^2=0.55$, $p < 0.001$). The estimated average effect of SST (95% confidence interval) on the beginning was: -11.4 ± 7.8 days/°C

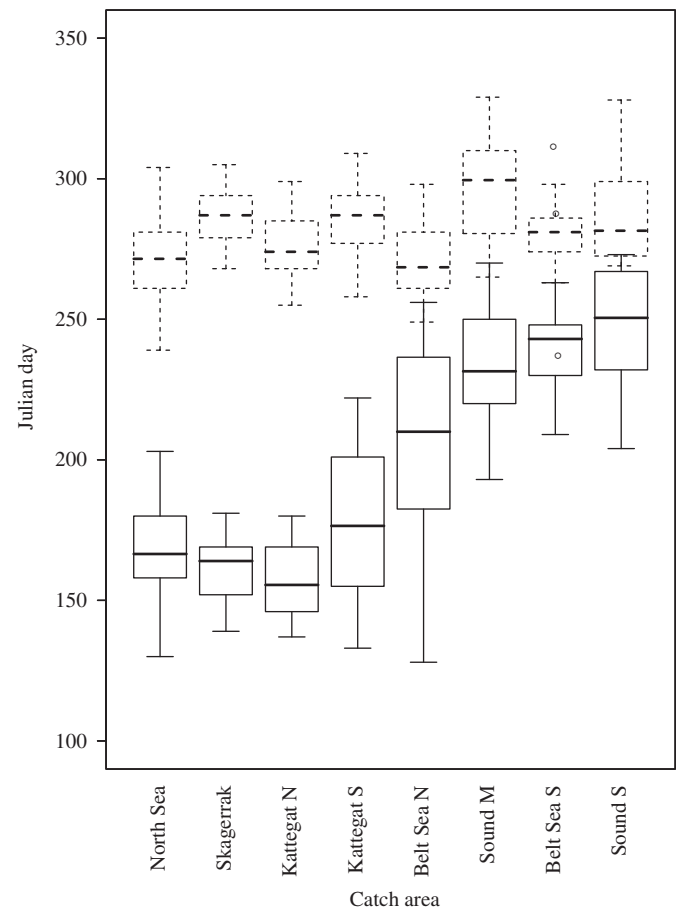


Fig. 7. Timing of migration of mackerel by area. Solid lined boxes: arrival (day of 10% percentile catch). Dashed boxes: departure (day of 90% percentile catch). Box plots indicating: median, quartiles, maximum and minimum.

and -7.5 ± 4.2 days/°C on the peak. Data and regression line are given in Fig. 9.

3.6. Temperature dependent egg production

The timing of the egg production peak was significantly correlated with SST ($R^2=0.31$, $p < 0.04$). The estimated average effect of SST (95% confidence interval) on peak spawning time was: -2.3 ± 2.1 days/°C. Data and regression line are given in Fig. 10.

4. Discussion

Our analyses have demonstrated a strong relationship between sea surface temperature in the North Sea, the timing of spawning of the North Sea mackerel and the timing of the post-spawning migration. Sea surface temperature was shown to be strongly positively related to the temperature at the depth of spawning and egg development. Furthermore, the sequential and size dependent timing of the appearance of mackerel supports the anecdotal information about an eastern post-spawning migration of North Sea mackerel.

The areas closest to the wintering and spawning areas, the North Sea, Skagerrak and Kattegat N, are the first areas where the cumulative landings exceeds 10% of the total annual landings. This happens approx. 2 month (67 days) later in the Belt Sea and the Sound. Mackerel arrives first in the west (Belt Sea N) and then in the east (the Sound N), perhaps because the speed of migration is

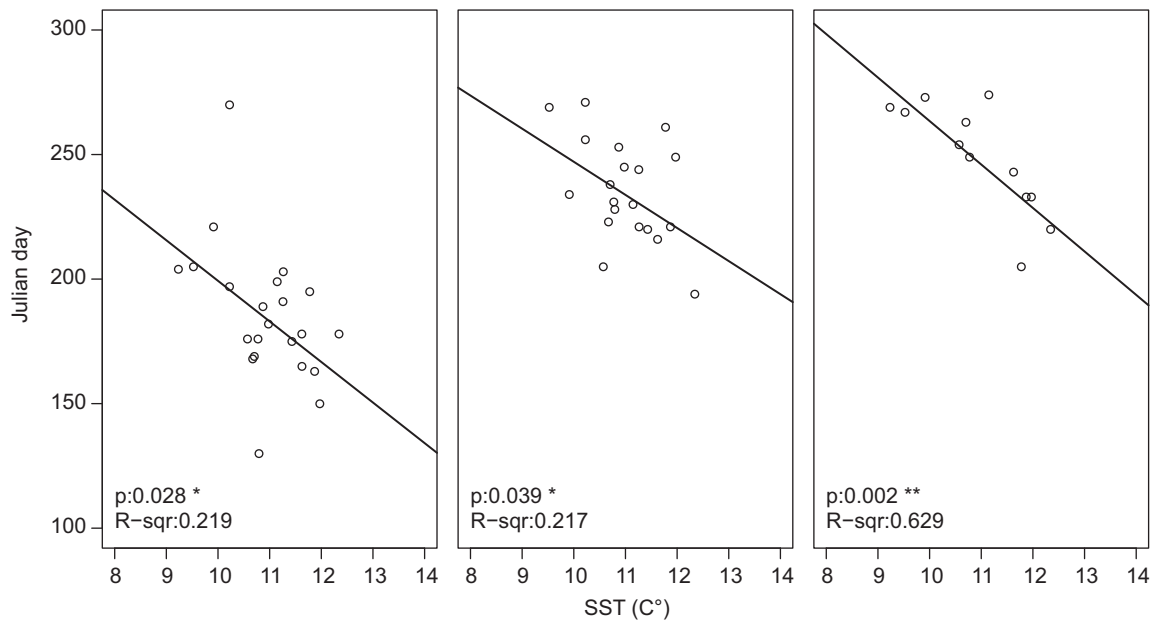


Fig. 8. Arrival time of mackerel vs. sea surface temperature in May–June in the North Sea spawning area. From left: arrival in North Sea (large mackerel only), the Sound N and the Sound S.

Table 2

Significant relations between temperature and the arrival time of mackerel in different areas and for different months. *P* values in bold indicate that the relation is plotted in Fig. 8.

Size	Area		Season (month)				
	Catch	SST	Winter (12, 1, 2)	Pre-spawning (3, 4)	Begin and peak spawning (5, 6)	Late spawning (7)	Post-spawning (8)
Large	North Sea	North Sea			0.028		
All	Kattegat N	North Sea					0.020
	Sound N	North Sea			0.039		
		Skagerrak			0.033		
		Kattegat			0.020		
Small	Sound S	North Sea		0.045	0.002		
		Skagerrak		0.047	0.006		
		Kattegat		0.047	0.014		
	North Sea	North Sea				0.007	
	Skagerrak	North Sea	0.012	0.004			
	Kattegat N	North Sea					0.019
		Skagerrak					0.023
		Kattegat					0.017
	Kattegat S	Skagerrak		0.049			
		Kattegat			0.050		

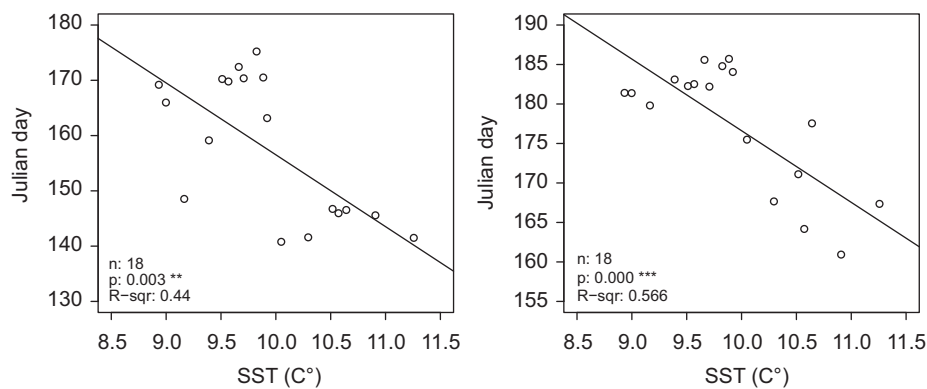


Fig. 9. Timing of mackerel larvae occurrences corrected for temperature dependant growth. Left: beginning vs. SST (May–June). Right: peak vs. SST (June).

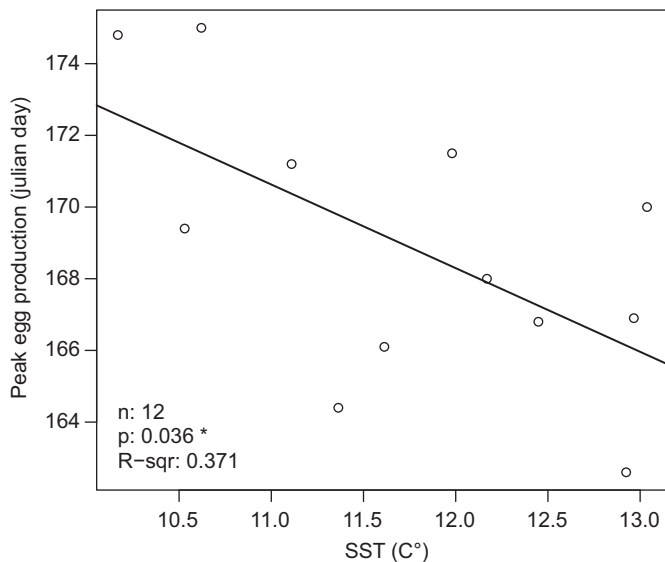


Fig. 10. Peak spawning time of mackerel estimated from egg survey data vs. sea surface temperature (°C) in June in the North Sea spawning area.

higher in the shallower and more saline western part of Kattegat and/or because the wider opening into Belt Sea N makes it easier for mackerel to pass into this area than through the narrow entrance to the Sound with the strong currents between Helsingør and Helsingborg.

For the return migration the lack of a significant difference between departure dates in most areas was somewhat surprising given the knowledge about the winter/spawning migration of the southern/western components (Reid et al., 2001, 1997; Walsh et al., 1995). One reason for the almost simultaneous disappearance could be that mackerel move off-shore and/or into deeper waters out of reach of the small coastal vessels. No landings data from deeper waters was available to test this hypothesis, but the coastal landings data did not show any significant relationship with the temperature in the deeper waters (represented by CTD data from Skagerrak—details not included here). Another reason could be that the quality or quantity of food decreases. The departure date in the Sound N took place later than elsewhere, perhaps because larger mackerel may feed on the massive occurrences of herring in the Sound in late autumn (Dahl and Kirkegaard, 1986; Nielsen et al., 2001). Incidental commercial catches taken in winter in the Sound N, Kattegat and Skagerrak and catches obtained in the first quarter IBTS survey show that some individuals also overwinter here.

Large mackerel arrived (left) the Skagerrak and Kattegat significantly before (after) small mackerel. These results correspond to the observations by local fishermen, who state that the first of the arriving mackerel in the Sound are the largest (H.J. Trab, Personal Communication, 10 March 2010). Tagging has shown that juvenile mackerel of the south/western component does not migrate as far as the adults (Uriarte et al., 2001) and in the Norwegian Sea it is the larger fish that reach furthest to the North and West during the feeding migration in summer (Anon, 2009; Holst and Iversen, 1992; Nøttestad et al., 1999). From the western area it is known that larger mackerel spawn earlier than small (Dawson, 1986) and this, in combination with the increase in swimming speed with length (Pepin et al., 1988); may explain the size-specific migration pattern.

The timing of the arrival in the Sound N and S was related to temperature during the beginning and peak of spawning (May–June) and this produced an up to two months difference in arrival time between warm and cold years. It is noteworthy that arrival times in the Sound N and S are related to the temperature in the

areas the population has migrated through and spawned in, well before entering the Sound N and S, and not to local summer SST (data analysis details not provided here). Given this and, as a consequence of the size-specific migration, these early mackerel have most likely been adult; indicating that the time of their spawning is affected by temperature. Furthermore, the same relation was found for large (adult) mackerel on the North Sea coast. The arrival time in Belt Sea N however was not significantly related to temperature. However, explorative analysis showed a significant relation between arrival time and the North Sea temperature in April–May, a signal that disappeared in the final temporal stratification. Furthermore arrival in the Belt Sea N, like along the North Sea coast, and the Sound S and N was significantly related to the timing (first day of 9°) of the warming in the spawning area (results not provided here). A similar relation to the temperature in the spawning area was not found for migration through the wider areas of Skagerrak and Kattegat; perhaps because of a poorer signal-to-noise ratio due to feeding taking place more off-shore and out of reach of the majority of the small vessels.

Where the landings data provided a proxy for the initiation of spawning, CPR data on larval occurrence provided the same information as well as a proxy for peak spawning, and so did the egg survey. All four analyses rejected the null hypothesis of no relation to temperature. To get the same result from three completely independent data sources, strengthen the conclusion considerably. However, although the size of the effect did not differ significantly between analyses it was associated with considerable uncertainty. The effect estimated from the landings data was largest, perhaps because temperature also affects the migration speed.

We minimized the bias in the estimates of the time of first arrival caused by interannual changes in abundance, fishing effort and catchability using a fixed percentage of the cumulative annual landings as the arrival criteria. However, this could not fully remove the effect of interannual changes in the seasonal distribution of fishing effort and changes in gear technology. In order to minimize these effects, we included only landings from small-scale coastal fisheries using vessels of a length less than 10 m. The rate of technological change, and hence overall catchability, increases with vessel length (Eigaard, 2009). Hence, for the small vessels we do not anticipate that changes in gear technology will influence our results significantly and several of the fisheries included, such as fixed pound nets, have not changed much through time. For other fleets where changes in technology may have affected catchability a detailed analysis is impossible due to the lack of logbook data. Bias may also be introduced if catches are taken outside the area to which the port of landing belongs. This bias is also minimized by only including small vessels whose operation radius is small.

Mackerel originating from the western and southern spawning components are known to migrate into the North Sea, where they are caught summer, autumn and winter. The recapture of four individuals off the Norwegian and Swedish coasts of Skagerrak (Uriarte et al., 2001) out of a total of 1592 recaptures of the 161,115 tagged individuals of western and southern mackerel constitutes the only evidence that these components may migrate further east and enter the study area. However, all four individuals were recovered later in the year than the arrival times calculated in this study. The limited number of recaptures furthermore points to a very restricted entry of these mackerel; they were therefore assumed not to influence the conclusions in this study.

By timing the spawning and subsequently the onset of the feeding season; temperature thus affects migration together with size. A range of other factors such as current speed and direction (Castonguay and Gilbert, 1995), food abundance and distribution, or presence of predators could also affect migration.

The conclusions in this study differ from earlier studies of the relationship between mackerel and temperature in the North Sea

(Greve et al., 2005; Jacobsen, 2006), perhaps as a result of the larger and improved data sets analysed here. The difference between our results and the results obtained in studies of the southern spawning stock (Punzon and Villamor, 2009) could, however, reflect a real pattern. If mackerel monitors a suite of spawning triggers, such as temperature, light, food and internal maturation, and all have to pass a threshold, then the limiting factor could differ between areas. Both internal physiological triggers such as temperature dependent gonad maturation and external factors such as food abundance and quality have been shown to affect the spawning of marine fish species (Hutchings and Myers, 1994; Tomkiewicz et al., 2009; Wieland et al., 2000). A spawning strategy that maximizes egg and larval fitness would aim at providing the optimal combination of low mortality, good feeding opportunities and adequate temperature. Mendiola et al. (2006) found the cumulative mortality during the egg phase to increase below 11 °C. For larvae high temperatures result in high growth rates (Bartsch, 2002), but at the cost of a higher food demand. If the food supply is insufficient the larvae will starve and their mortality increase. In the southern areas mackerel larvae have been shown to be abundant at the time of the spring phytoplankton bloom, while the larvae in the North Sea occur later in the year. In the North Sea, close to the northernmost limit of observed mackerel spawning, temperature could therefore be the limiting factor. However, changes in temperature in the North Sea might also impact mackerel recruitment through the food web by changing the species composition and temporal abundance of different planktonic groups (Drinkwater et al., 2010; Edwards and Richardson, 2004). This subsequently affects the spatiotemporal match/mismatch between mackerel larvae and their food; an aspect that have been shown to have a strong effect on the recruitment of other fish species (Beaugrand et al., 2003; Cushing, 1990).

The present results have several implications for the management and monitoring of mackerel. Changes in the timing of mackerel spawning and migration can have a large effect on results from surveys being performed at a fixed time of the year, this has been the case for the Mackerel egg survey (ICES, 2010) and the acoustic spring survey for mackerel in the Bay of Biscay (ICES, 2009b; Punzon and Villamor, 2009). More generally, in a climate change scenario where temperatures increase, our results show that the timing of important events in the life cycle of North Sea mackerel will change, with likely impacts on both the growth, reproduction, distribution and productivity of the stock.

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Appendix III

Migration and Fisheries of North East Atlantic Mackerel (*Scomber scombrus*) in Autumn and Winter

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Abstract

It has been suggested that observed spatial variation in mackerel fisheries, extending over several hundreds of kilometers, is reflective of climate-driven changes in mackerel migration patterns. Previous studies have been unable to clearly demonstrate this link. In this paper we demonstrate correlation between temperature and mackerel migration/distribution as proxied by mackerel catch data from both scientific bottom trawl surveys and commercial fisheries. We show that mackerel aggregate and migrate distances of up to 500 km along the continental shelf edge from mid-November to early March. The path of this migration coincides with the location of the relatively warm shelf edge current and, as a consequence of this affinity, mackerel are guided towards the main spawning area in the south. Using a simulated time series of temperature of the shelf edge current we show that variations in the timing of the migration are significantly correlated to temperature fluctuations within the current. The proposed proxies for mackerel distribution were found to be significantly correlated. However, the correlations were weak and only significant during periods without substantial legislative or technical developments. Substantial caution should therefore be exercised when using such data as proxies for mackerel distribution. Our results include a new temperature record for the shelf edge current obtained by embedding the available hydrographic observations within a statistical model needed to understand the migration through large parts of the life of adult mackerel and for the management of this major international fishery.

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Introduction

Changes in global climate and the aspiration for sustainable fisheries management have highlighted the requirement for improved understanding of the effects of the marine climate on the behaviour of important fish species [1]. Mackerel (*Scomber scombrus*) is an abundant migratory pelagic fish in the north-east Atlantic, where it plays an important ecological role by feeding on zooplankton and on the pelagic larval and juvenile stages of a number of commercially important fish stocks [2,3]. Furthermore, mackerel is itself targeted by whales, fish and a large pelagic fishing fleet with annual landings of between 500 000 and 1 000 000 tonnes [2,4]. The largest mackerel fishery targets and follows mackerel aggregations throughout autumn and winter. Marked historical changes in the timing and spatial distribution of this fishery have been observed, but remain unexplained [4–7]. The fishing fleet is composed of modern pelagic trawlers and seiners that use sonar to locate schools of adult mackerel and are highly mobile, regularly steaming hundreds of kilometres from port. As a result of this adaptive behaviour, it is feasible that the observed changes in the timing and spatial distribution of commercial landings are representative of the spatiotemporal dynamics of the mackerel population.

It has been hypothesized that temperature is an important modulator of the autumn/winter spawning migration. An acoustic and oceanographic survey in December 1995 demonstrated

a relationship between the location of mackerel in the Northern North Sea prior to the onset of migration and the local temperature field [8]. It has also been noted that mackerel behaviour appeared to be related to temperature while the mackerel stayed to the north and west of the Shetland [9,10]. If the distribution of the fishery reflects the distribution of the mackerel and the mackerel distribution is related to the water temperature, then we would expect the temperature field to be reflected in the spatiotemporal distribution of the fishery. However, previous studies have not revealed any simple correlation between these variables [5–7].

Using fisheries independent data from scientific bottom trawl surveys and commercial landings statistics we investigate the mackerel migration from October to March and test

- i) whether data from commercial fisheries and scientific bottom trawl surveys can form the basis for useful proxies of the distribution of adult mackerel
- ii) whether changes in the temperature of the shelf edge current are related to the significant temporal and spatial variation observed in these proxies

We consider our results in the light of other factors that influence the fishing fleet behaviour such as fisheries development, legislation and distance to home port. Finally, we discuss our findings within a larger oceanographic context of circulation

patterns and global warming, review possibilities for hindcasts and forecasts, and implications for fisheries management.

Materials and Methods

Fisheries Data

Quarterly landings in the autumn-winter fishery were used as reported to the International Council for Exploration of the Sea (ICES). Due to the fact that the autumn-winter fishery overlaps two calendar years, first quarter landings were treated as being a '5th' quarter of the previous year. Thus, Q4 landings are those reported in October–December and Q5 corresponds to January–March of the following year. The study area encompasses the northern limit of the reported catches and includes the majority of the total reported catch (83% in Q4 and 56% in Q5) (Figure 1).

Commercial landings data were reported to ICES as quarterly totals per ICES statistical rectangle (1° latitude by 0.5° longitude). The position and time of the catch was assumed to be at the center of the reported rectangle and midway through the quarter. The landings consisted primarily (>95%) of adult fish [4].

To investigate the spatial variations in the behavior of the fleet the reported landings were projected onto a curvilinear 'Continental Shelf Edge' (CSE) axis in the style of [11], from 54.5 N 10.5 W in the south, and following the 200 m isobath, passing north of the Shetland Islands before turning south and following the Norwegian Trench into the North Sea (Figure 1). The total length of the CSE axis is approximately 1700 km. Each reported landing was projected onto the CSE axis by selecting the closest of 1000 equally spaced positions along the CSE axis. Distances were calculated based on great circle (WGS84 ellipsoid) distances. Both the position projected onto CSE axis and the distance of the reported landing from the axis were calculated and stored for further analysis.

The quarterly CSE axis distributions were then represented by a single metric for further comparison with temperature. Two alternative metrics were explored;

- the center of gravity of landings (CoG)
- the position of 50% cumulative landings (Po50%CL)

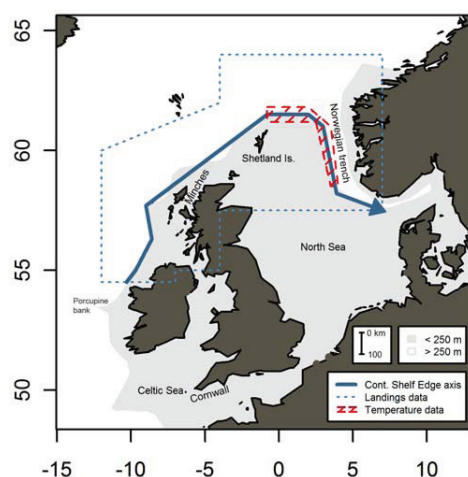


Figure 1. Map of study area and place names referred in the text. Continental shelf marked in grey (bottom depth <250 m). Blue polygon indicates the study area. Blue bold arrow shows the Continental shelf edge axis. Red shaded area marks the area of temperature profiles.

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CoG was calculated by year and quarter as the weighted average of distances. The weighting factor was the mass (in kg) of each projected landing record. Po50%CL was calculated as the position along the CSE where the cumulative landings represented 50% of the total landings by year and quarter.

A literature survey and an interview with the skipper of a vessel that fished throughout the study period were carried out in order to identify periods where changes in the behavior of the commercial fishery were driven by factors other than mackerel behavior.

Bottom Trawl Survey Data

Data from international bottom trawl surveys (IBTS) carried out in quarter 1 (January–March) between 1985 and 2011 on the shelf out to 500 m were downloaded from the ICES repository (<http://datras.ices.dk>). The study area was limited to the area described for the commercial landings. Relatively few mackerel were caught outside the study area, e.g. in Kattegat/Skagerrak [12] and over 90% were from surveys in March. Further south, in the Bay of Biscay, mackerel arrive at the spawning grounds around the time of this survey [13]; the present dataset therefore covers the northern part of the NEA mackerel population. Catch per Unit Effort (CPUE) of adult mackerel was calculated as catch in numbers per trawl hour, where adult mackerel were defined as being longer than 27 cm (most mackerel first spawn at the age of 2 (58%) and the mean length at age 2 in Q1 west of Scotland is 27 cm [4]). For ease of comparison with the commercial landings dataset, first quarter surveys were treated as being a '5th' quarter of the previous year. Hauls were projected onto the CSE axis as described for commercial landings and the CoG and Po50%CL of CPUEs calculated.

Temperature Data and Modelling

In the present study, we investigate links between water temperature and mackerel distribution that could support the hypothesis of a temperature-driven migration. The continental shelf edge current which flows along the shelf edge to the northwest of Scotland, north and then east of the Shetland Islands, along the western edge of the Norwegian trench and into the northern North Sea, is warmer than both the surrounding coastal waters and the oceanic waters off the shelf during winter (Figure 2) [8,9]. It is the temperature of this water mass that is of interest in this study. Unfortunately, relevant observations are not available for the entire study period. A relevant temperature record was therefore obtained by embedding the available hydrographic observations within a statistical model. The modelled area is shown in Figure 1 and was selected because it is the coldest area of the warm core of the current (Figure 2) and therefore the area where cold avoidance by mackerel would be most pronounced. Also, there are a significant number of observations available for this area.

It is within this core of relatively warm water in the northern North Sea that acoustic surveys found mackerel to aggregate in 50–220 m depth in early winter [8–10,14]. Due to the fact that water is cooled throughout the winter, both downstream (along) and away from the CSE, temperature was modeled with year, day of year, distance parallel (CSE) and perpendicular (dCSE) to the CSE axis as explanatory variables i.e:

$$\begin{aligned} \text{Temperature} = & \beta_4(\text{Year}) + \beta_3 S_3(\text{Day}) + \beta_2 S_2(dCSE) \\ & + \beta_1 S_1(CSE) + \beta_0 + \epsilon, \end{aligned}$$

where *CSE* is the distance along the CSE axis from the start of the

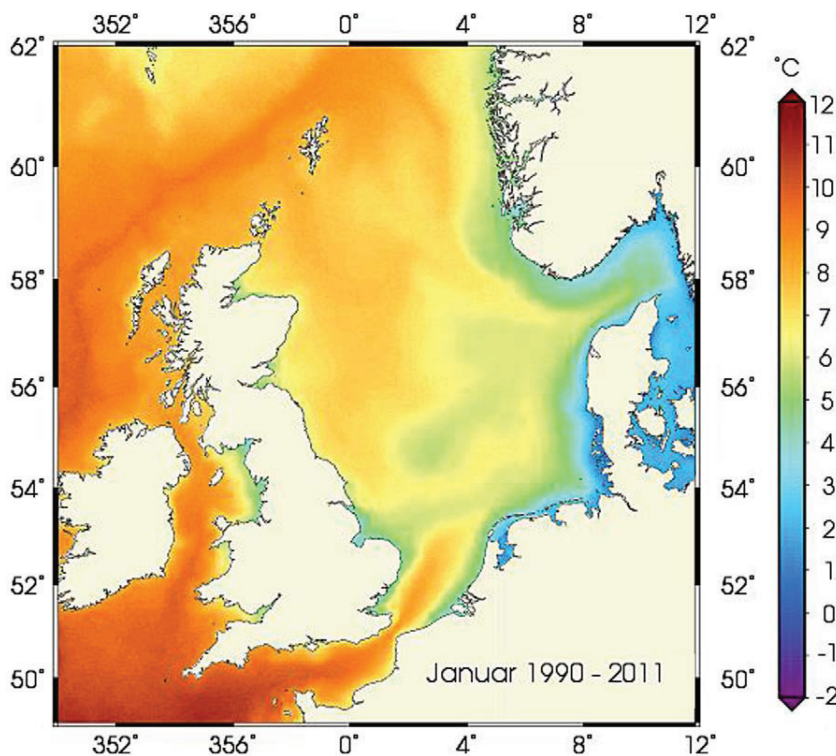


Figure 2. Map of average sea surface temperature in January 1990–2011 showing the relatively warm high-saline eastern Atlantic water flowing north-eastwards on and along the continental shelf edge, flanked by cooler water masses. Temperature measurement measured by satellite and mapped with permission from Bundesamt für Seeschifffahrt und Hydrographie, Germany (www.bsh.de). doi:10.1371/journal.pone.0051541.g002

axis (in the south) to the projected sample position, $dCSE$ is the distance from the sample site to the projected position, day is the number of days elapsed in the year, from 1st of February (day 32) to 31st of January (Day 386). $Year$ is the year of the observation and, $S()$ is the penalized cubic regression spline smoothing function implemented in the “mgcv”-R-package as cardinal spline [15]. Day , CSE and $dCSE$ were thus modeled as smoothed predictor variables with smoothing parameters (k =number of “knots”) set to 3, in order to allow for a non-linear temperature development through the season and along the CSE whilst avoiding overfitting, whilst $Year$ is treated as a categorical factor (i.e. one parameter per year). 1056 temperature profiles from CTD stations and bottle sampling between November and January were downloaded from the ICES hydrographic database [16] and used to fit the model using the “mgcv” package in R [15]. Model building was done by sequentially removing non-significant parameters (i.e. those with $p>0.05$). The final model was then used to predict a time series of temperatures in early winter (15th of December), at the center of the area (1326 km along CSE axis from starting point) where mackerel were known to be present [8].

For validation purposes, we compared the GAM temperature time series with

- a similarly modeled time series further upstream (west of Scotland, 35 km from CSE in the area 55–65°N 10°W–5°E) in February–March, and
- a coarser modeled and validated dataset of sea surface temperatures (SST) obtained from the Hadley Centre SST data set (HadSST2) [17], by averaging over a larger geographical box covering the North Sea–SE Norwegian Sea area

(55°N– 65°N, 0–5°E) and including the months from November to January.

Finally, correlation analysis of the mackerel distribution metrics described above and modelled temperature field were performed. All correlation analyses were adjusted for autocorrelation if this exceeded the 95% confidence limits of white noise ($\pm 2\sqrt{N^{-1}}$, where N is sample size) [18]. Adjustments were done by substituting the degrees of freedom with the effective number of degrees of freedom [19].

Results

The final temperature model identified $Year$, Day of $Year$ and CSE as significant explanatory variables. In line with expectations, temperature decreased through the winter (Figure 3, $p<0.001$) and downstream along the CSE axis (Figure 4, $p<0.001$). The modeled temperature time series shows an overall increase throughout much of the study period with a decrease in the most recent years (Figure 5). The model explained 81% of the variance in the data (adj. $R^2=0.81$). Parameter estimates for all years are given in table S1. As a rough validation for the overall development of the temperature time series, we found it to be significantly positively correlated to a modeled temperature time series in the area west of Scotland in February–March 1985–2010 ($P=0.005$, $R^2=0.36$, Figure S1, same GAM model structure as the primary temperature series), and also to the Hadley time series of sea surface temperature in November–January 1948–2010 ($P<0.001$, $R^2=0.48$, Figure S2).

There was a strong tendency for commercial and bottom trawl catches to be associated with the area along the CSE axis, with

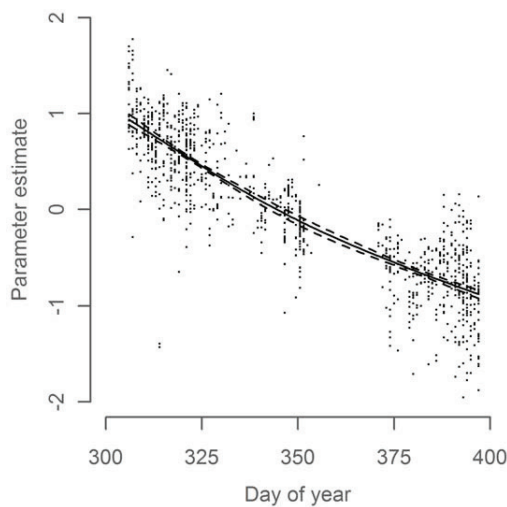


Figure 3. Day of Year parameter in the temperature model. Parameter estimate (solid line) with 95% confidence interval (dashed lines) and partial residuals (dots) relative to mean predicted value. doi:10.1371/journal.pone.0051541.g003

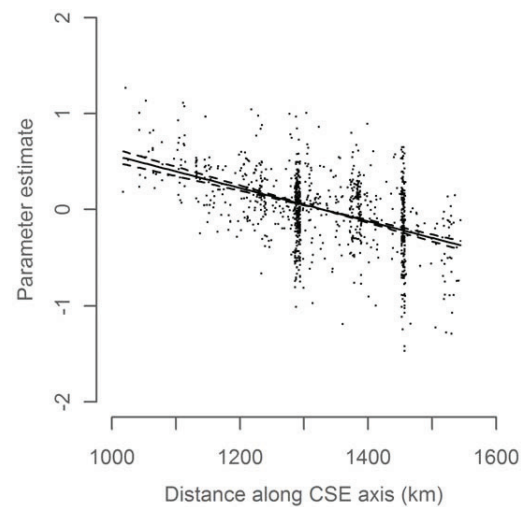


Figure 4. CSE parameter in the temperature model. Parameter estimate (solid line) with 95% confidence interval (dashed lines) and partial residuals (dots) relative to mean predicted value. doi:10.1371/journal.pone.0051541.g004

74% of the commercial landings in Q4, 92% in Q5 and 87% of the survey catches were taken within a 75 km distance of the CSE axis (Figure 6). We therefore chose to reduce the complexity of the spatial distributions by disregarding the across-axis information, *i.e.* considering the catches projected onto the CSE axis. Visual inspection of Center of Gravity (CoG) and Position of 50% Cumulative Landings (Po50%CL) overlaid on the distributions (Figure 7) indicates that both metrics are appropriate representations of the commercial landings and survey catches.

Landings in Q4 followed a consistent spatial pattern with generally small variance within and between years (Figure 7, left). Landings in Q5 and especially bottom trawl survey catches show greater variance (Figure 7, mid-right).

A progressive southwesterly shift along the CSE axis is evident in the commercial landings data from quarter 4 to 5 (Figure 7, left-mid) and also in the survey catches in late Q5 (Figure 7, right). The average shift of the CoG was found to be 360 km from Q4 to Q5, and 140 km from landings in Q5 to the survey in late Q5.

On a decadal scale, commercial landings (Figure 7, left-mid) show spatial shifts of the commercial fisheries over several hundreds of kilometers, consistent with that reported in the literature [4].

A literature review and an interview with an experienced fishing skipper with first-hand experience of the mackerel fishery during the study period (Tables 1, 2), suggests that factors other than the distribution of mackerel could have influenced the behavior of the fishing fleet, particularly for the Q4 fishery between 1990–1995 and also prior to 2000 for Q5 (see Tables 1, 2). After the collapse of the North Sea Mackerel stock in the 1970s, management measures were put in place in an attempt to protect the remainder of the population [20]. However, since Western and North Sea mackerel mix and are present in the northern North Sea at various times of the year, effective area based management proved difficult. Individual country quotas restricted vessel movements and their ability to target the migrating mackerel. Compounded by the temporal and spatial variability in the migration, this led to significant misreporting of commercial catch between areas IVa and VIa (and to a lesser extent between IIa and IVa), especially during the 1990s. Incremental changes were made to the management regimes in an attempt to mitigate this misreporting,

including partial relaxation of the area-based quotas, modifying area closures, and increased monitoring of the fishery.

Further data analysis was restricted to periods where the influence of management measures on the fleet behavior was expected to be minimal. This restricted the landings data from Q5 to only 10 observations (2000–2009), and is therefore why we draw our main conclusions based on the correlation analysis of landings in Q4 and scientific surveys.

The spatial development of the fishery (Figure 7) during these periods, shows i) a southwestern distribution in Q4 in 1977–1989, ii) a steady northeastern distribution in 2000–2007 (Q4+Q5), followed by iii) a movement toward southwest in 2008–2010 (Q4+Q5). Detailed maps of relative distributions of commercial landings and CPUE from bottom trawl survey in these three periods confirm this pattern (Figure 8). Annual maps of relative

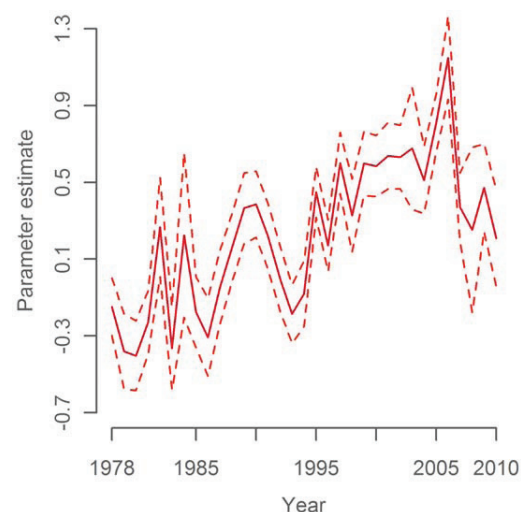


Figure 5. Year parameter in the temperature model. Parameter estimate (solid line) with 95% confidence interval (dashed lines) relative to mean predicted value. doi:10.1371/journal.pone.0051541.g005

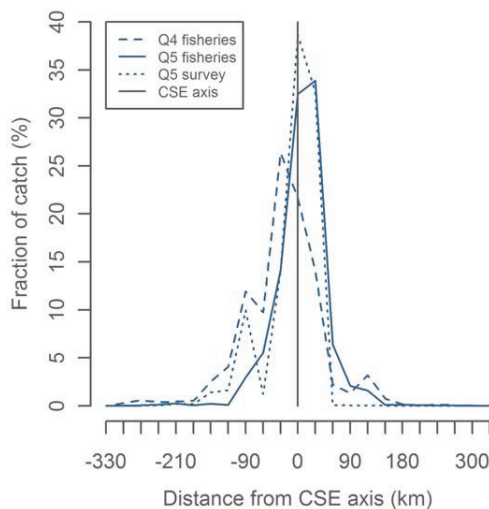


Figure 6. Distance from catch position to continental shelf edge (CSE) axis. Positive values are off the shelf. In the North Sea positive values are northeast of the axis.
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distributions as well as annual and periodic maps of actual catches are given in Figure S3.

An examination of the consistency between the three Po50%CL proxies for spatial distribution showed significant positive correlations between the quarter 4 fisheries and the quarter 5 trawl survey (1985–2010 ex.1990–1995, $p = 0.031$, $R^2 = 0.23$). This was also the case when the quarter 4 and quarter 5 fisheries were analysed (2000–2009, $p = 0.040$, $R^2 = 0.43$). However, no significant correlation was found between the short time series of commercial landings in Q5 and the trawl survey (2000–2009, $p > 0.05$).

Comparisons of the modelled temperature time series with the Po50%CL proxies for mackerel distribution (Figure 9) reveal

a significant positive correlation with fisheries-independent surveys (1985–2010, $p = 0.007$, $R^2 = 0.27$), and with commercial landings in Q4 from 1977–2010 (ex. 1990–1995) ($p < 0.001$, $R^2 = 0.59$), but not with the short time series of commercial landings in Q5 (2000–2009, $p > 0.05$). Correlation analyses are summarized in table 3.

Discussion

Our analyses demonstrate that when the NEA mackerel return in late summer from the feeding areas on the European shelf and in the Nordic Seas [4], they aggregate through autumn and early winter along the continental shelf edge, where they are targeted by commercial trawlers and purse seiners. Later in winter the commercial fleets and the fisheries independent bottom trawl survey find the mackerel further towards the southwest. The path of the migration, as suggested by the location of commercial and survey catches coincides with the location of the relatively warm high-saline eastern Atlantic water flowing north-eastwards on and along the continental shelf edge, flanked by cooler water masses. We present a modelled new time series of temperature in this current and find it to be significantly correlated with two proxies for spatiotemporal mackerel distribution. The proxies are derived from data over a significant period of time and a large proportion of the European shelf and encapsulate large scale changes in distribution. Our results indicate that

- the mackerel population is found further upstream in warmer waters as the current cools through winter
- this process is associated via climatic variability, with large impacts on the mackerel migration and fisheries, and suggest a mechanism where
- this affinity for warm water leads the mackerel towards the main spawning areas.

These results are in accordance with earlier studies of mackerel during autumn and winter [5–10].

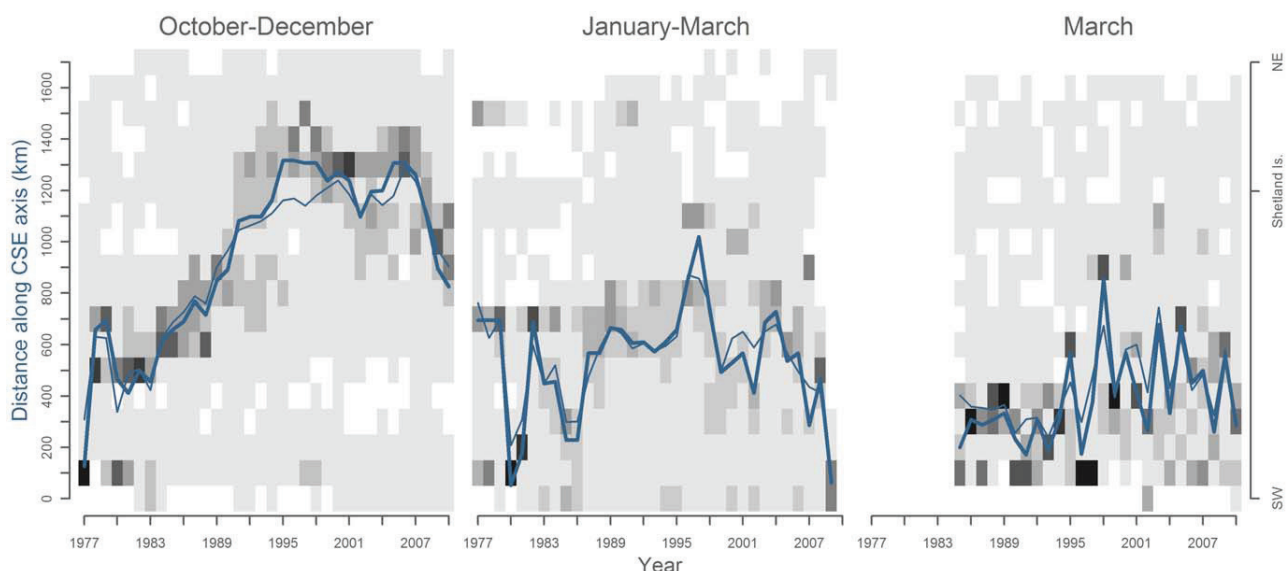


Figure 7. Hovmöller plot of mackerel distributions proxies from commercial landings in October to December (left), January to March (mid) and bottom trawl surveys in March (right). The spatial aspect have been reduced to one dimension by projecting the catch location onto the CSE axis. Greyscale in cells range in 10%-steps from 0–10% (white), to 90–100% (black). Thick line represents position of 50% cumulative landings (left, mid) or CPUE (right) and thin line shows the center of gravity of the distances.
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Table 1. Factors affecting spatiotemporal distribution of the commercial fishery in Q3–4.

Years	Q3–4
1977–1983	Landings data reflected the traditional Q3 Norwegian fishery in the Northern North Sea, and the development of Q3 fisheries more coastal to Eastern Scotland and in the Minches.
1984–1995	The Q3 landings reflect a putative temporal and spatial change in fish availability. Main landings were caught progressively later (ending up in Q4) and north-eastwards from 1983 to 1997 [7]. The large north-eastwards shift from the mid-1980s to mid-1990s occurred in times when fisheries were developing and legislation were changing. However, fisherman observations confirm the spatial development of the fishery was, at least in the beginning, a response to changes mackerel migration patterns as they encountered the mackerel progressively further north-east (Pers. Com. Capt. Alex Wiseman, July 2011). This statement seems reliable, because if the mackerel had been available further north-east in the late 1970s and early 1980s, it would have been economically beneficial to fish on those schools rather than steaming all the way to the Minches from the pelagic ports in north-east Scotland. Later, this fishery (now a Q4 fishery) fluctuates between the coast of Norway and the Shetlands, but remains predominantly east of 4°W.
1996–2010	From about 1996 onwards the fishery was well established in Q4, and its movements through this period was not known to be affected by other large changes than movements of the mackerel stock.

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The present work illustrates the limitations associated with the available data and underlines that caution should be exercised when utilising catch data as a proxy for distribution. The relatively low trawling speed and small scale trawls employed by standardized scientific surveys are unsuited for catching a fast pelagic species like mackerel. Furthermore, changes in vertical distribution and schooling behaviour reduce the signal-to-noise ratio in the trawl survey data and contributes to the low levels of explained variance (R^2) in correlations that include this variable. In contrast, commercial fishing employs much more efficient methods. Commercial landings data are, however, only appropriate for inferring changes in stock movements over time when other factors remain relatively constant. This was not the case for the Q4 fishery between 1990 to 1995, when the management regime restricted the ability of vessels to target fish migrating through areas IVa and VIa and fisheries technology and techniques changed the behaviour and increased the efficiency of the fleet (Table 1). An approach to circumvent this problem has been used in a previous study, where high resolution catch data from a validated subset of the fleet showed that the observed change from late 1970s to late 1990s leveled out from 1989 to 1994 [5]. This is consistent with our conclusions, as this was the period where fisheries and temperature deviated (Figure 9).

Other major changes in mackerel fisheries have occurred through the period 1977–2010, such as the summer fishery in Icelandic waters that commenced in recent years [4]. While this fishery is outside the main scope of this study, it is related to the

westward expansion of the summer distribution [21]. Changes in the summer distribution could lead to a change in the path taken during the return migration in late summer and early autumn, which could potentially affect the autumn-winter distribution. Further investigation of this effect is therefore warranted.

The results presented are in accord with recent investigations that link climatic variability and spatiotemporal dynamics of mackerel spawning [12,22,23,33]. Mackerel differ from most other exothermal organisms by being i) purely pelagic through all life stages, and ii) relatively fast and constantly swimming [24], able to react to the environment by migrating over long distances. This dynamic spatial behavior enables the mackerel to avoid poor temperature conditions during its migration in search of optimal areas for reproduction and feeding. This seems to be most evident during the cold season when other constraints such as feeding and reproduction are reduced or absent. The effect of temperature on the spatial shifts of the mackerel distribution is suggested to be on a scale of hundreds of kilometers during winter (Figure 9), much larger than in spring where spawning has been moving only 40 km north per °C [23] and in summer where polar water merely forms an outer boundary of the extremely large area occupied by mackerel [4,25]. It is understood that the primary activity during winter is the maturation of eggs and sperm. It may be that the specific temperature conditions selected by the mackerel are an adaptation to optimize development of reproductive products. The present findings facilitate testing of this hypothesis and exploration of further importance for spawning.

Table 2. Factors affecting spatiotemporal distribution of the commercial fishery in Q5.

Years	Q5
1977–1983	Fishery was predominantly in the Cornwall area. However, in this period a new fishery was developing to the north-west of Ireland and west of Scotland
1984	The area around Cornwall was then closed in 1984 to protect the juveniles in this nursery area
1985–1990	The bulk of the landings were from the north of Ireland and west of Scotland moving progressively northwards. The fishery were mainly targeting adult mackerel when they were resident in an area or migrating slowly. However, during this period, development of the pair-trawling technique facilitated the fishery on fast migrating mackerel. Movement of landings in this period may therefore represent a development of the fishery as well as a movement of the stock.
1991–1999	Landings are clustered west of 4 W. This may reflect area misreporting from further east, as the northern North Sea was closed from 31 st December.
2000–2010	From 1999 legislation were changed to allow fishing in the northern North Sea up to the 15 th of February, and even though this should have ended area misreporting (as the fish were available in the northern North Sea at this time) there appears to have been a “habit” of misreporting to a series of rectangles on the 4 W line which persisted [35].

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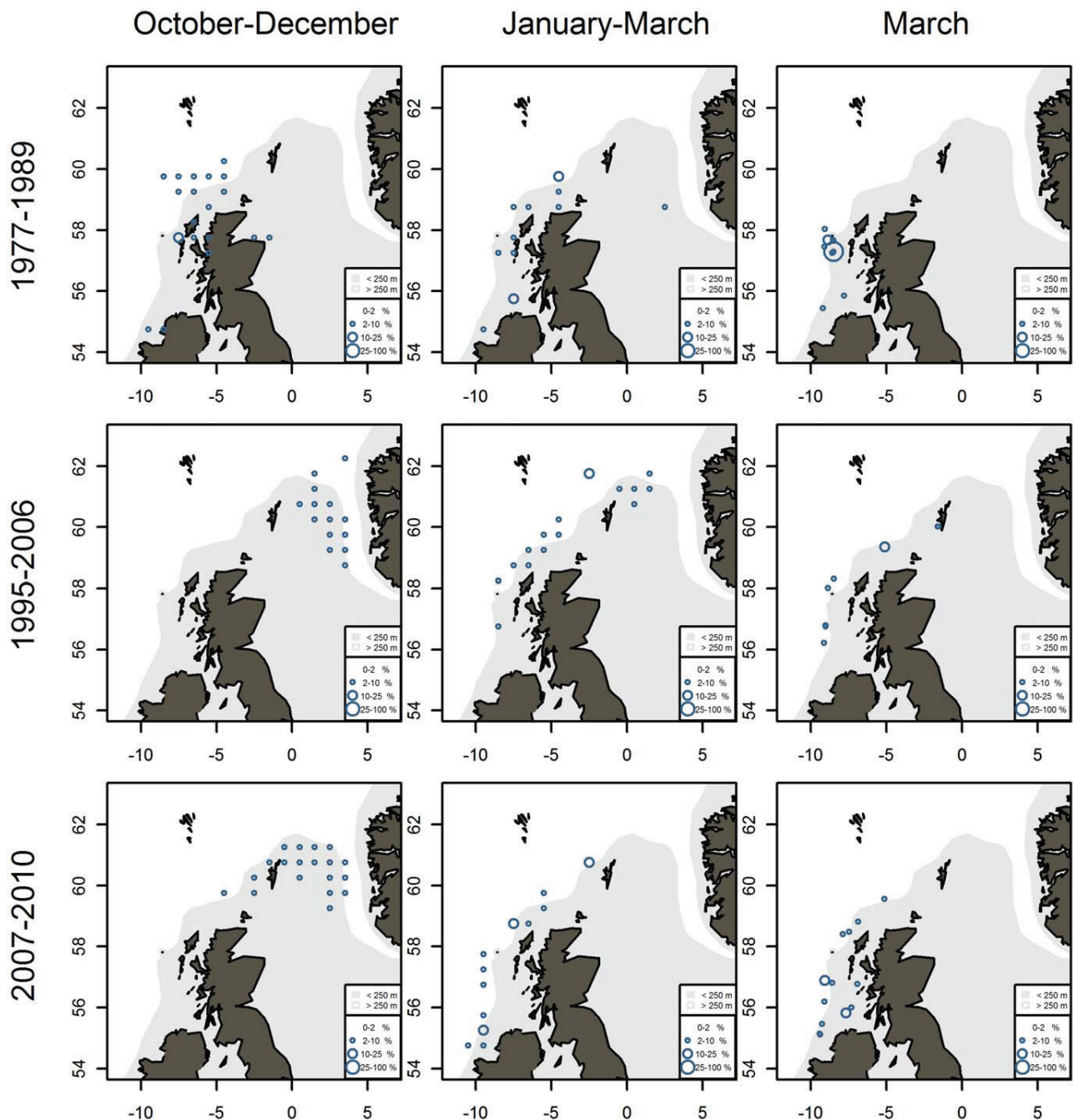


Figure 8. Relative distribution of mackerel landings from the commercial fisheries and mackerel catches from fisheries independent bottom trawl surveys. Data from January–March are shifted back one year to match data in the same season from October–December.

doi:10.1371/journal.pone.0051541.g008

The physical environment within the shelf edge current is related to large scale oceanographic circulation patterns. Conditions in the Bay of Biscay and the European shelf seas, to the east of the continental shelf edge current, are related to the Northern Hemisphere Temperature trend [26]. This differs from the oceanic region west of the shelf edge current, which to a greater extent is regulated by the dynamics of the subpolar gyre [27,28]. The physical environment within the shelf edge current is related to the northern hemisphere temperature type of variability, but

may also be influenced by the oceanic domain during periods when the subpolar gyre circulation is particularly strong, such as during the period 1990–1995 [27]. The shelf edge waters are furthermore modulated by smaller sub-decadal oscillations, caused by pulses of eastern water from the Bay of Biscay [29]. Once warm and saline anomalies have passed the Porcupine Bank, the geographic divide between the subtropical and the subpolar gyres, they are destined to continue northward as baroclinic Rossby waves [30,31], with an advection time of one-two years, to the

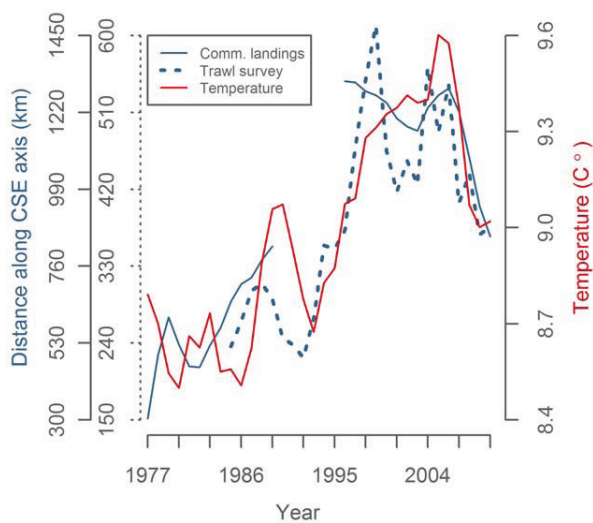


Figure 9. Mackerel distribution and temperature trends (3y rm). Position of 50% cumulative landings in Q4 and in survey CPUE along the continental shelf edge axis (blue) and temperature around the shelf edge in the Northern North Sea from off Shetland Is. to the western edge of the Norwegian trench in November–January (red). doi:10.1371/journal.pone.0051541.g009

entrance of the Nordic Seas [27,32]. This oceanic inertia holds promise for making projections one-two years into the future. Shorter-term predictions may be possible based on measurements of the temperature further “upstream”: such predictions could be of value for the fishing industry as it may reduce the time spend on searching for mackerel. However, detailed forecasting of mackerel behavior outside the observed temperature range is not possible before any additional causal effects and their interactions are sufficiently clarified.

The results presented have implications for the management, fishery and monitoring of mackerel. Recent changes in mackerel distribution have resulted in political disputes over zonal attachments and led to a break-down of the international management agreements since 2008. Furthermore, in 2009 fishermen were taken by surprise when the mackerel had departed the northern North Sea east of 4° (which separates management areas IVa and VIa) by October [34], significantly earlier than in previous years. As a consequence, quotas worth over 100 M € could not be utilized in that year by the Norwegian and Danish industries [35] whilst, at the same time, Scottish seiners had little difficulty in catching the mackerel further west. We have demonstrated that cooling of the continental shelf edge current, possibly triggered this early migration. In a climate change scenario where temperatures increase further, our results suggest that mackerel distribution is likely to be affected with subsequent effects for the fishery and mackerel prey.

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Table 3. Correlation analyses between proxies for spatial patterns of the mackerel represented by Position of 50% Cumulative Landings (Po50%CL) and modeled temperature in the shelf edge current.

	Landings Q5	Trawl survey	Temperature
Landings Q4	$p = 0.040, R^2 = 0.43$	$p = 0.020, R^2 = 0.25$	$p < 0.001, R^2 = 0.58$
Landings Q5		$p > 0.05$	$p > 0.05$
Trawl survey			$p = 0.007, R^2 = 0.27$

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Supporting Information

Figure S1 Temperature time series from November–January 1977–2010 northern North Sea used in the analysis of mackerel distributions (solid line as 3 year running mean). Temperature time series from February–March 1985–2010 west of Scotland (dashed line as 3 year running mean). Both series modeled as described in material and methods. (TIF)

Figure S2 3 year running means of temperature time series 1948–2010. Red: Primary temperature series in November–January northern North Sea. Modeled as described in material and methods for the shorter time series. Black: Hadley sea surface temperature anomaly in November–January 55–65 N 10 W–5 E (black). Data from Hadley Centre SST data set (HadSST2) [17]. (TIF)

Figure S3 Mackerel landings from commercial fisheries and mackerel catches from fisheries independent bottom trawl surveys. Data from January–March are shifted back one year to match data in the same season from October–December. (TIF)

Table S1 Table with temperature model parameter estimates. (DOC)

Acknowledgments

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Author Contributions

Analyzed the data: TJ. Wrote the paper: TJ AC CK HH MRP.

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Appendix IV

Natal homing of North Eastern Atlantic Mackerel (*Scomber scombrus*) as revealed by juvenile growth patterns

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Abstract

Juvenile growth patterns indicate inter-cohort natal homing behaviour among North East Atlantic mackerel. This means that a significant proportion of a given year class will return to spawn at higher latitudes, than other individuals from the same year class that were hatched at lower latitudes. Comparison of growth data (fish length) with latitude shows that southern juvenile mackerel attain a greater length than those further north before growth ceases during their first winter. A similar significant relationship was found between the growth in the first year (derived from the inner winter ring on otoliths) and latitudes for adult mackerel spawning between 44°N (Bay of Biscay) and 54°N (west of Ireland), a finding consistent with natal homing. No such relationship was found in mackerel spawning at more northerly latitudes, possibly as a consequence of increased spatial mixing in a more energetic regime. This study contributes to the understanding of mackerel migration behavior and hence to the spatiotemporal distribution dynamics around spawning time.

Introduction

Mackerel (*Scomber scombrus*) is one of the most abundant and widely distributed migratory fish species in the North East Atlantic [1]. Knowledge of the population structure of an exploited fish species is key to understanding its basic population biology and a necessary prerequisite for providing effective advice to fisheries managers. The population structure of mackerel has consequently been the subject of repeated studies over the last 100 years of mackerel science [2,3].

The North Eastern Atlantic mackerel (NEAM) stock has traditionally been divided into 3 separate spawning components; a southern, western and North Sea component [4]. NEAM mainly spawn on the continental shelf from Biscay in the south to the west of Scotland and in the North Sea. While the southern and western spawning areas are connected, the North Sea area is spatially separated by reduced spawning in the English and Fair Isle channels [5]. Most studies on natal homing have concentrated on identifying differences between mackerel in the North Sea and in the west, in order to demonstrate that mackerel return to spawn in the same area where they hatched. The results of such studies have, to date, failed to conclusively demonstrate natal homing in these stock components. While the initial analyses were based on landing statistics [3], more recent approaches have attempted to distinguish between individuals based on geno/phenotypic classification. Unfortunately, some of the studies on characteristics such as juvenile growth patterns in otoliths [6,7], protein polymorphism [8,9] and tapeworm (*Grillotia smarigora*) infection rates [10] were based on individuals from the respective spawning area that were *not* all in the process of spawning (*i.e.* ripe/running). Due to the fact that mackerel migrate from the western areas into the North Sea, before spawning in the North Sea has ceased [11], these studies may therefore have included mackerel from several discrete components. Consequently, conclusions on natal homing and the existence of multiple components cannot be drawn

from these studies. Other studies were correctly based on spawning individuals, but found no difference in ectoparasite infections [12], blood phenotypes [13], gene variants [8] and (unlike in the west Atlantic [14]), otolith shapes (Jansen unpubl. analysis of 652 spawning mackerel). In recent years, modern genetic approaches have been applied, but with inconclusive results. While mitochondrial DNA from relatively few spawning mackerel did not group into the expected clades, statistical analysis of the same allele frequencies separated the 3 western samples from the rest providing some, albeit weak, support for genetic differentiation on an ecological time scale [15]. A more recent work on mackerel genetics does not support a separation (Pers.Comm. Frode Lingaas, 21 Sept. 2011). In conclusion, there is presently no support for the hypothesis of multiple separate natal homing components /stocks/contingents within the wider NEAM population.

In this study, we test the hypothesis of natal homing, by following spatially related growth patterns from early life to spawning adults in the North East Atlantic.

Key factors affecting somatic growth of mackerel larvae and juveniles may vary with latitude throughout the wide spawning area. The length increment during the first year of growth can be postulated to be dependent on the date of birth, and on the growth rate, which is influenced by ambient temperature and food availability. Since mackerel spawn earlier at southern latitudes, the first growth season is longer for southern mackerel. Also, ambient temperatures are generally higher at southern latitudes, allowing for faster growth rate, but also higher energy requirements. Given that NEA mackerel does not initiate size dependent migratory behaviour prior to maturation [11], we can therefore hypothesise that the body-size of juvenile mackerel are negatively correlated with latitude at the end of the first growth season. We therefore test the null-hypothesis:

H_0^1 : *Growth from hatch to first winter is not related to latitude for juvenile mackerel of age 0.*

If mackerel are natal homing and H_0^1 is rejected, then the spatial pattern of first year growth would be preserved through all ages. We therefore test the null-hypothesis:

$H_0^2 : H_0^1$ is true or growth from hatch to first winter is not related to latitude for spawning mackerel.

In the event that both null hypotheses are rejected, we can reject panmixia and conclude that NEA mackerel have a tendency for some type of natal homing. However, we will not be able to distinguish between *absolute spatial homing* (e.g. as with salmon) and *inter-cohort relative natal homing* (spatial natal homing relative to other individuals from the same year class), as the observed growth patterns could appear while the entire mackerel population moved north-south from year to year due to variable environmental conditions.

We test H_0^1 with a dataset of body length during the first winter. H_0^2 is tested with measurements of otolith growth from hatch to first winter. Otolith growth during the first growth season is used as a proxy for somatic growth based on the strong correlation between mackerel body length and otolith length at the end of the first growth season [7]. The structural properties of otolith growth and formation allows for measurement of the first growth zone in mackerel of any age.

Materials and methods

Mackerel length growth

Mean body length by quarter and ICES subarea were used as reported annually to the International Council for Exploration of the Sea (ICES). The data were obtained from tables in the annual mackerel assessment reports (e.g. [1]). Samples originate from both commercial fisheries and scientific surveys. Only data from the first quarter (January-March) were used in the final analysis because initial data

exploration indicated that growth had not ceased in the fourth quarter (October-December). The available length observations were averaged by stratum, i.e. by year, quarter, ICES subarea and country by the individual national sampling programs before reporting to ICES. While length observations are usually expected to be log-gaussian distributed, we could assume that mean length (\hat{l}_i) in stratum i has a gaussian distribution with a mean vector μ and standard deviation σ due to the relatively high number of observations (mean = 2455):

$$\hat{l}_i \sim N(\mu_i, \sigma_i^2)$$

We tested hypothesis H_0^1 by modelling length with the following predictor variables:

- *Latitude* (considered to be the center of the appropriate ICES subarea)
- *Spawning component* (= North Sea or South-west). Mackerel in the North Sea might be a separate spawning component [1,17].
- *Year*. Including a year effect permits interannual environmental variation (food, temperature, currents etc.) to be considered.

Since mean length can only be positive, we expressed the systematic effect as:

$$\log(\mu_i) = \beta_0 + \beta_1 \cdot \text{Latitude}_i + \beta_{SC_i} + \beta_{y_i}$$

where SC_i is the spawning component and y_i is the year of the i 'th observation

The lack of individual length observations complicated the error term in the model. We addressed this by modeling the variance as the sum of the individual errors due to sampling (σ_s^2) and model implementation (σ_m^2). Since the variance of the mean is equivalent to the variance of the individual

observations divided by the number of averaged observations, the variance of a mean length in stratum i can be written:

$$\sigma_i^2 = \sigma_m^2 + \sigma_s^2 / n_i$$

Which leads to the following model formulation:

$$\hat{l}_i \sim N(\exp(\beta_0 + \beta_1 \cdot \text{Latitude}_i + \beta_{SC_i} + \beta_{y_i}), \sigma_m^2 + \sigma_s^2 / n_i)$$

The *corvif* function of the AED R-package was used to calculate Variance Inflation Factors (VIF). VIFs are indicators of collinearity. The predictor variables were sufficiently independent to be used in the same model fit, if the VIFs were > 3 [18]. Model parameters $\beta_{0,1,2}$, β_{SC_i} , β_{y_i} , σ_m and σ_s were estimated using the Nelder-Mead method for identifying the maximum likelihood model.

In order to ensure that a latitude-length relation at the end of the first growth season is not a consequence of size-differentiated migration, we also explored the variability of this relationship through the first two years of growth.

Mackerel otolith growth

Sagittal otoliths extracted from mackerel caught by commercial vessels and scientific surveys in 2002-2003 and 2005-2006 were examined. The archived otoliths were embedded in resin (histokitt). Otoliths were viewed in reflected light under a stereo microscope (Leica MZ6) and images digitised (Leica DFC320 camera and Leica IM 50 frame grabber) using a standard setup of exposure (107.9 ms, 8 bits/channel with a frame of 1300×1030 pixels), light intensity, angle and direction of illumination. The length of the first winter ring (L1) was measured as the distance between the anterior and posterior

centres of the first broad opaque band (Figure S 1) from otoliths taken from spawning mackerel (ICES maturity stage 6 *i.e.* “ripe or running”) from 2-11 years of age.

We subsequently tested hypothesis H_0^2 by modelling L1 with the following predictor variables:

- *Latitude* (numeric).
- *Spawning component* (Factor: North Sea / South-west). Mackerel in the North Sea might be a separate spawning component [1,17].
- *Year class* (Factor: Year - age). This year specific effect represents the interannual variation of environmental parameters that can affect growth rates (food, temperature, currents etc.).
- *Day of year* (Numeric). To account for seasonal effects.
- *Length* (numeric). To account for size based effects.
- 2nd order interactions.

Variance Inflation Factors (VIF) were calculated for the predictor variables to ensure that the model output was not affected by collinearity (VIF > 3) [18]. Multivariate linear regression modeling was done “backwards” by sequentially removing insignificant ($p > 0.05$) terms starting with 2nd order interactions.

The modelling was performed using R statistical software (version 2.12.1) incorporating the “stats”, “bbmle”, “nlme”, “nortest” and “AED” packages [19].

Results

The body length dataset consisted of 132 records of mean length by ICES subarea derived from 366,570 individual length observations. The available samples cover all ICES sub areas throughout the spawning and nursery areas from the Bay of Biscay to the North Sea region, over the period 1997 to 2010.

The only significant term in the model of mackerel body length at the end of the first growth season was *latitude*. We consequently can reject the H_0^1 hypothesis that growth from hatching until the first winter is not related to latitude.

In order to ensure that the observed relationship between latitude and body length after the first year of growth is not a consequence of size-differentiated migration, we investigated the variability of this relationship through the first two years of growth. While the earliest observations (July-September) confirmed the negative latitude-length relation, later observations (during the mackerel's second year) showed no significant correlation, consistent with spatial mixing (Figure 1).

The L1 dataset (first winter ring) comprised 1,265 individual measurements with samples broadly distributed throughout the spawning area from the northern Bay of Biscay to the North Sea region (Figure 2). As before, the only significant term in the model of L1 was *latitude*. We consequently reject the H_0^2 hypothesis (H_0^1 is true or growth from hatch to first winter is not related to latitude for spawning mackerel).

Inspection of the model residuals in both growth-latitude models revealed that the negative correlations were mainly evident from 44°N to around 54°N (Figure S 2-3). We therefore repeated the modelling steps separately for two geographical regions: 44°N -54°N and 54°N -61.2°N. While no significant terms were found in the northern models ($p>0.05$), we again found *latitude* to be the only significant term in the southern models (Table 1, Figure 3-4). Latitude was negatively correlated with body size and L1 with an estimated decrease of $9 \pm 5 \%$ and $10 \pm 3\%$ over the 8.5° from the Bay of Biscay to west of Ireland. The residuals of both models were normal distributed (Anderson-Darling normality test: $p>0.05$) and do not display any distinct patterns.

We consequently reject both H_0^1 and H_0^2 and accept the alternative hypothesis that relative inter-cohort natal homing is occurring.

Discussion

Our analyses demonstrate that, compared across latitudes, southern mackerel reach a larger size before growth ceases during their first winter. We found this relationship between latitude and growth in the first year to be significant both for juveniles of age 1 and for adults that return to spawn fish between the Bay of Biscay in the south and west of Ireland in the north (44°N -54°N). This means that, a significant proportion of a given year class will return to spawn at higher latitudes, than other individuals from the same year class that were hatched at lower latitudes. Any two mackerel that originate from different latitudes will therefore tend to return and spawn at different latitudes – not together. While we reject panmixia, we are unable to distinguish between absolute spatial homing (*e.g.* as with salmon) and *inter-cohort relative natal homing* (spatial natal homing relative to other individuals from the same years class), as the observed growth patterns could appear while the entire mackerel population moved north-south from year to year due to variable environmental conditions. However, any interannual meridional variability have apparently not been sufficiently strong to override the homing signal in the data even though we pooled mackerel from the year classes 1991 to 2006 in our analysis. On the other hand, zonal variation is not analysed for. Since mackerel are pelagic through all life stages, a more dynamic relative homing model where the mackerel seeks certain water masses and environmental regimes seems more realistic than a model where the mackerel are completely fixed by certain spatial structures.

The demonstrated relationship between latitude and the length of the first winter ring, confirms the results from a study on year classes from the 1970s [7]. However, as mentioned in the introduction, this study was not performed on spawning fish and therefore inconclusive due to the migration capabilities of mackerel. The latitude-growth relationship from our study were statistically significant only in the

area from the Biscay to west of Ireland. This area is partly a retention area and partly an area with weak northwards flow along the shelf edge, which reduces spatial mixing and thus preserves the growth rate patterns in the population. This is in contrast to the areas further north where the strong north Atlantic current hits the European shelf edge around Porcupine bank and turns northwards on and along the shelf edge. Mixing of larvae and juveniles from different spawning locations is therefore a likely explanation for the lack of spatial growth patterns in the area north of Porcupine bank. However, it is also possible that there is no latitude gradient in growth rates in this area.

The observed correlation between latitude and growth may be a result of several processes [7,29]. Lower temperatures and shorter growth seasons at higher latitudes [30] can be expected to result in lower growth rates [31,32]. Size-seasonal-specific mortality may also have an effect. The disadvantage of a higher metabolic and growth rate as experienced in the warmer southern waters is that larvae need to feed at a higher rate in order to keep up with the elevated energy consumption. Larvae that are unable to find sufficient nutrients subsequently starve and die. This is more pronounced in warmer than in cooler waters and could theoretically lead to the patterns observed in the present study. The principal conclusion of the study relies only on the observed correlation between growth and latitude – it is independent of the actual causal effects.

In the case that the tendency for natal homing of North East Atlantic mackerel had been sufficiently strong over an evolutionary time scale, then it should have led to genetic differentiation. However, previous studies have indicated a weak or complete lack of genetic and/or phenotypic differentiation. This suggests that, on an evolutionary time scale, the rate of mixing has been too high in relation to the homing effect for genetic differences to become apparent. Further work on the balance between isolation and mixing and the effects on genetic differentiation on long term evolutionary vs. short term ecological time scales is needed.

The North Sea mackerel have traditionally been considered as a separate stock because spawning in the North Sea is spatially separated from that of the western and southern components and because of the significant localized depletion [17,33]. The lack of subsequent rebuilding in the North Sea during decades of high abundance in the southern/western areas could indicate isolation. However, the present approach did not provide the opportunity to show separate homing behavior for the North Sea and the areas west of Scotland, because the growth patterns were similar and there are relatively few samples available from the North Sea for the purposes of this study.

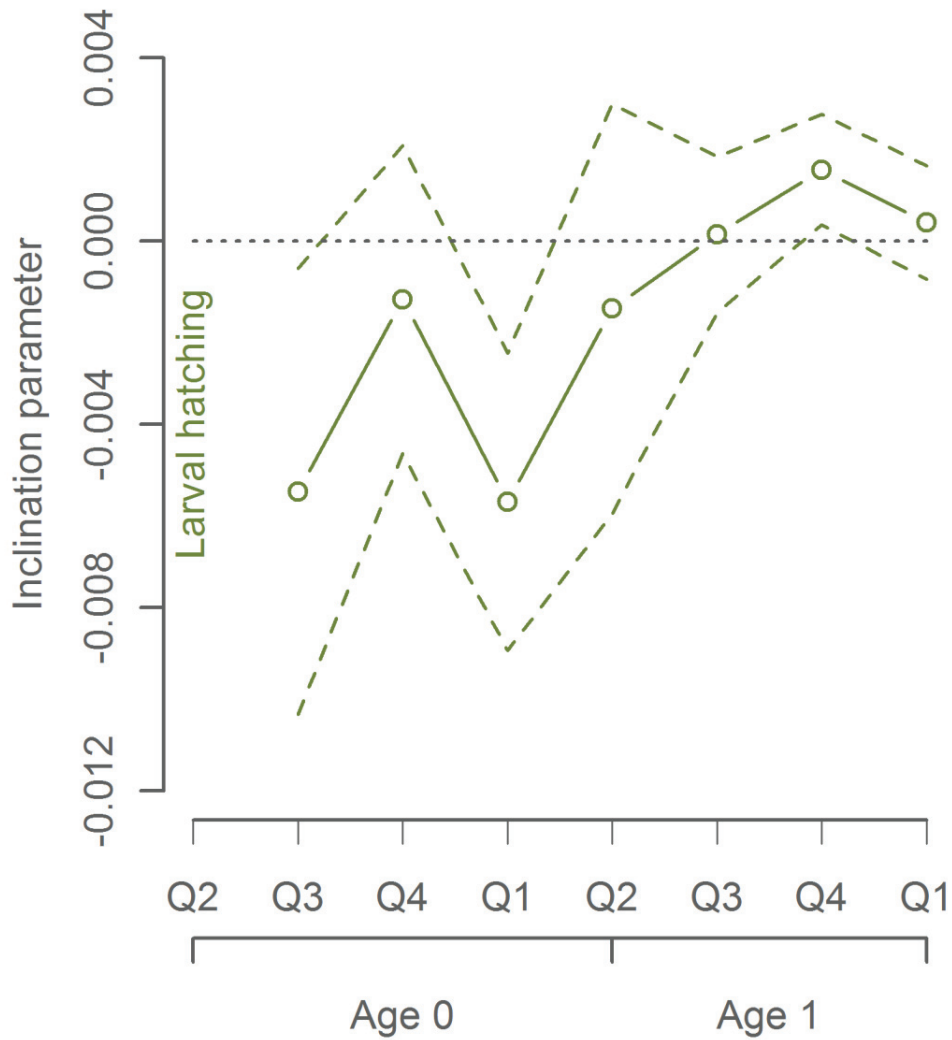
Homing behaviour is fundamental for life cycle closure therefore, also for separation into multiple contingents within a metapopulation. This is well known for other migrating pelagic species, such as the intensively studied herring [41,42]. While most herring contingents are natal homing [34], albeit with some mixing with other contingents [35,36], few are panmictic [37,38]. Genetically, there is very little difference between stocks (or contingents) [36][39] [40], indicating a fair level of mixing. Improved understanding of the dynamics of marine fishes requires knowledge of population level processes, and recent modeling studies demonstrate the importance of taking contingent specific exploitation rates into consideration in fisheries science and management [43,44]. However, inferring the exploitation of individual contingents is greatly complicated when the contingents mix at various rates during the year resulting in disproportionate exploitation over time and space. The current level of understanding of mackerel life cycle diversity with regards to homing, mixing [45] and metapopulation structure is currently lacking for advanced metapopulation management plan simulations. Sustainability and maximum sustainable yield may be compromised if such complex patterns are reduced through generalized management (e.g. area closures) that overlooks spatiotemporal population dynamics throughout the life cycle.

This study is the first to demonstrate natal homing behavior in mackerel – an important step towards understanding mackerel life cycle diversity and possible metapopulation structure.

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Figures



Fig

Figure 1. Latitude-length relation by mackerel age. Early life observations during the first year show negative latitude-length relations, while later observations show no significant correlation. The inclination parameter (β_1) on the Y-axis are the effect of latitude in the model $\log(\text{mean body length}) = \beta_0 + \beta_1 * \text{Latitude} + \beta_y + \varepsilon$, where β_y is the year-specific effect and ε is the random error term.

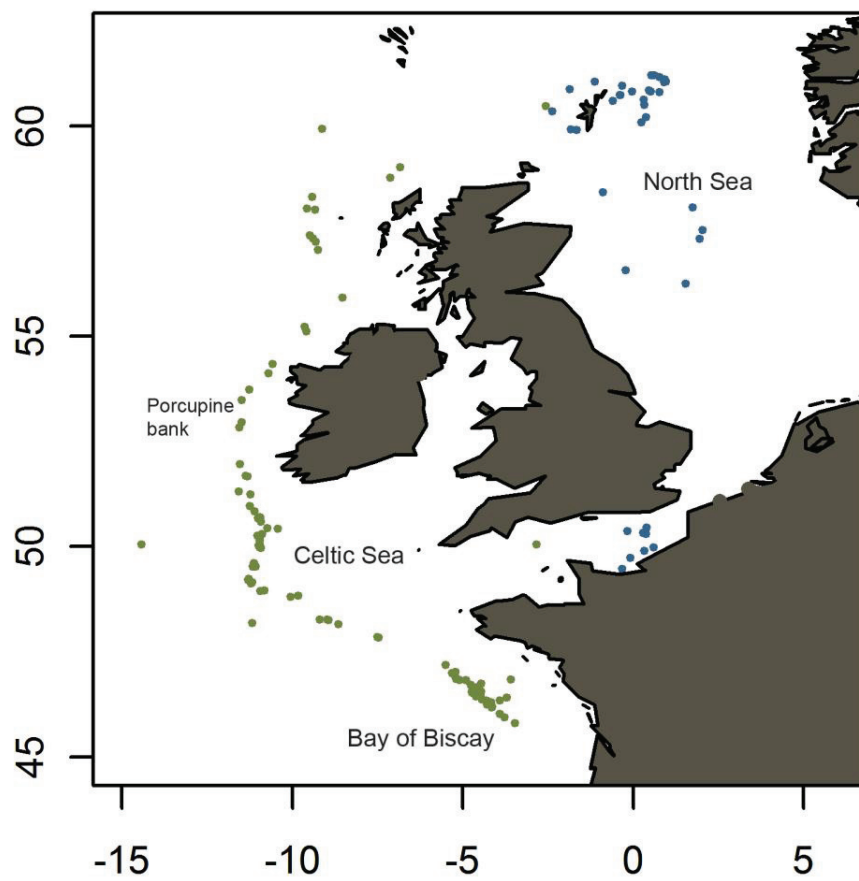


Figure 2. Otolith sample locations and geographical names referred to in the text.

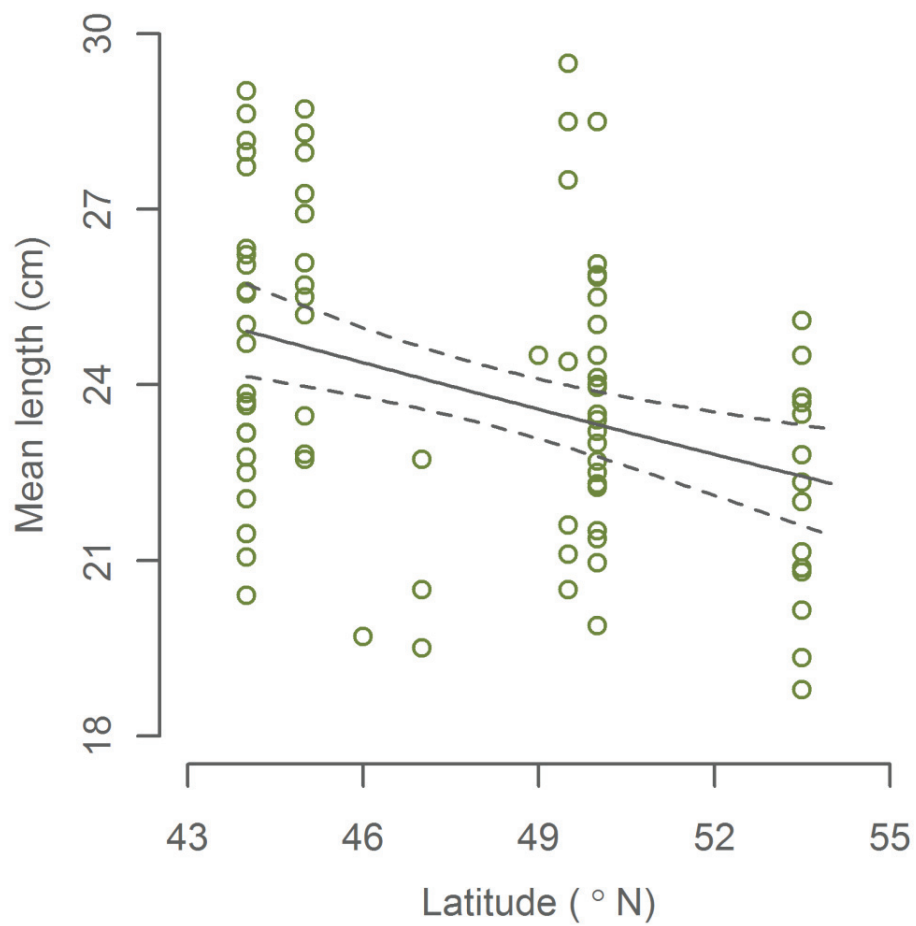


Figure 3. Mean body length of mackerel at the end of the first growth season (January-March) by latitude. 95% confidence interval indicated by dashed lines.

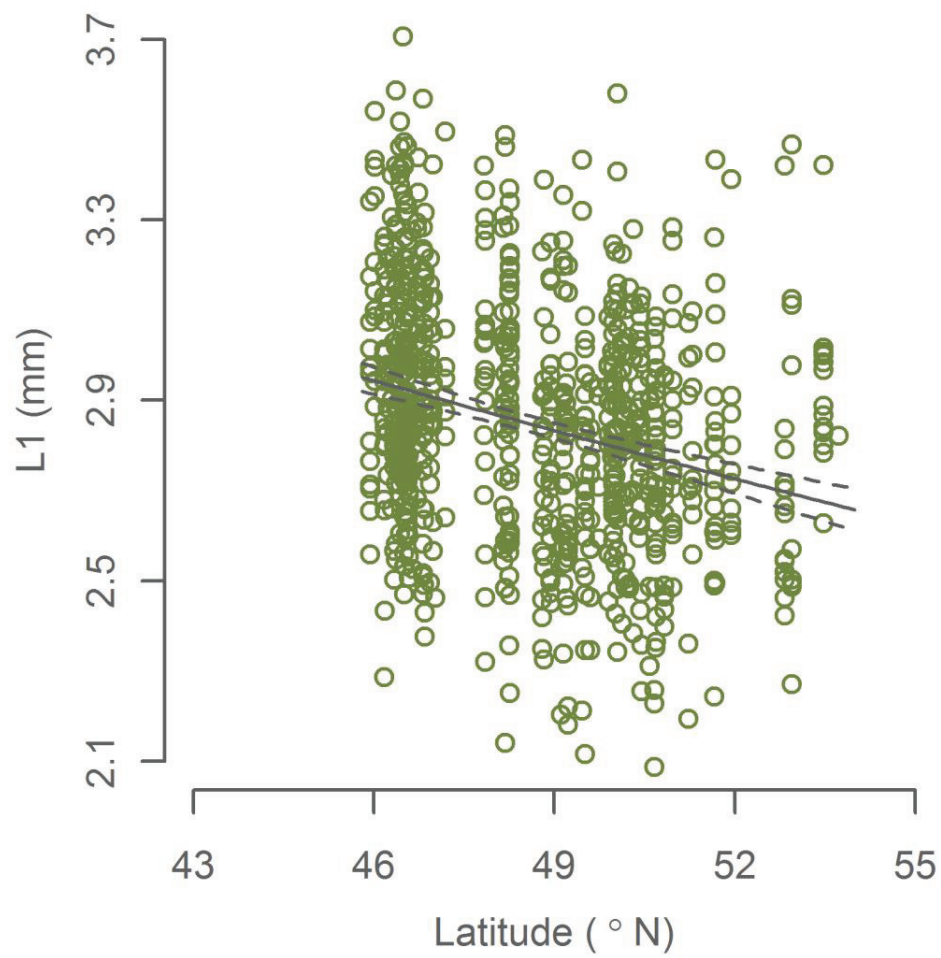


Figure 4. L1 (otolith growth from hatch to first winter) from spawning mackerel by latitude . 95% confidence interval indicated by dashed lines.

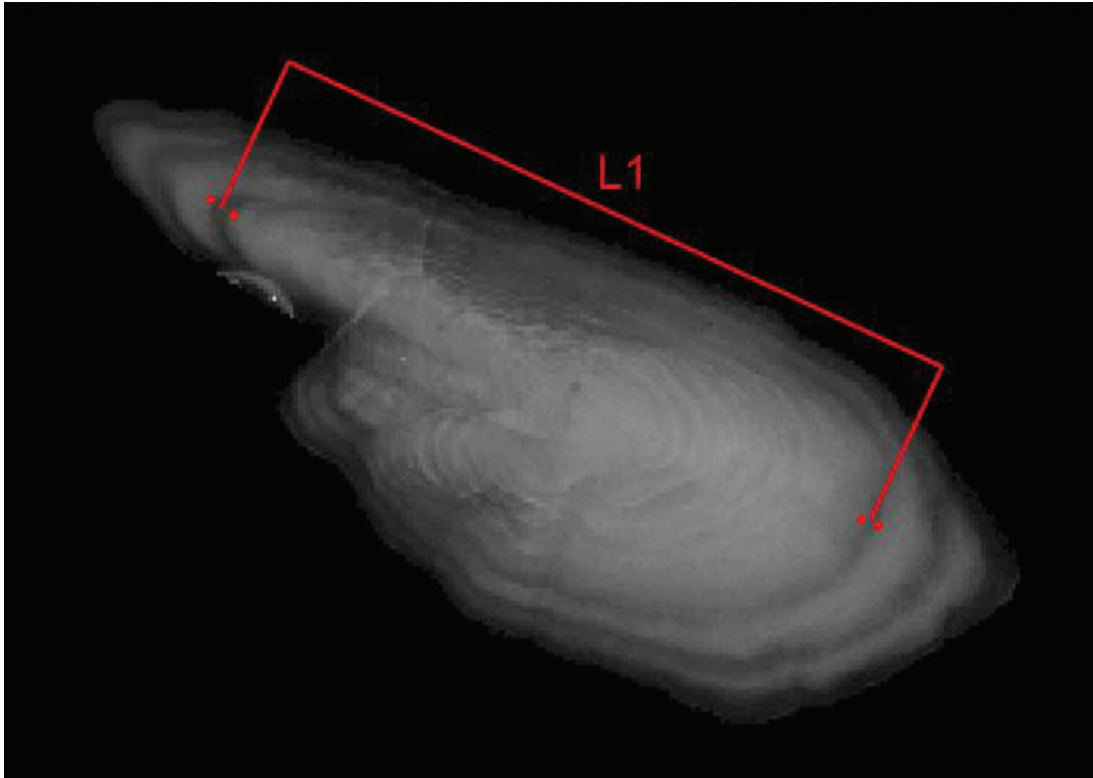


Figure S 1. Sagittal otolith showing L1 (otolith growth from hatch to first winter).

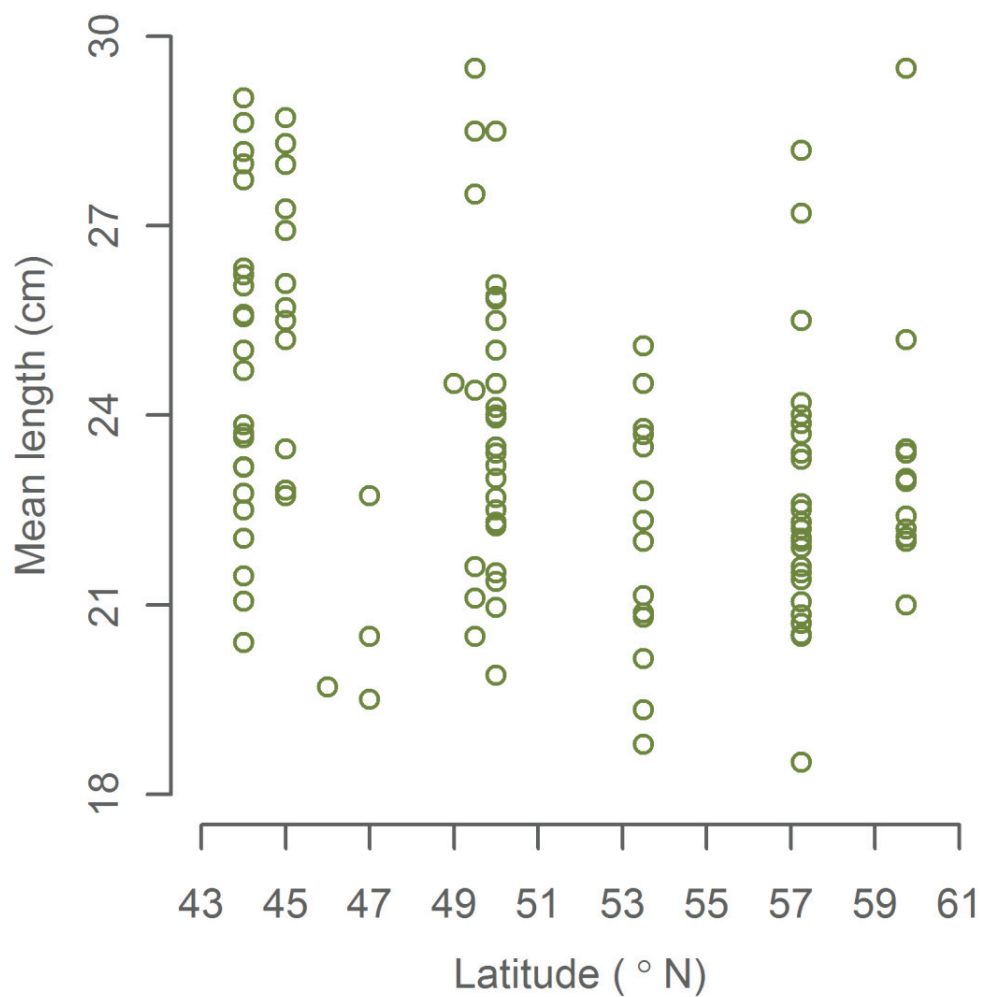


Figure S 2. Mean body length of mackerel at the end of the first growth season (January-March) by latitude (including 54-61°N).

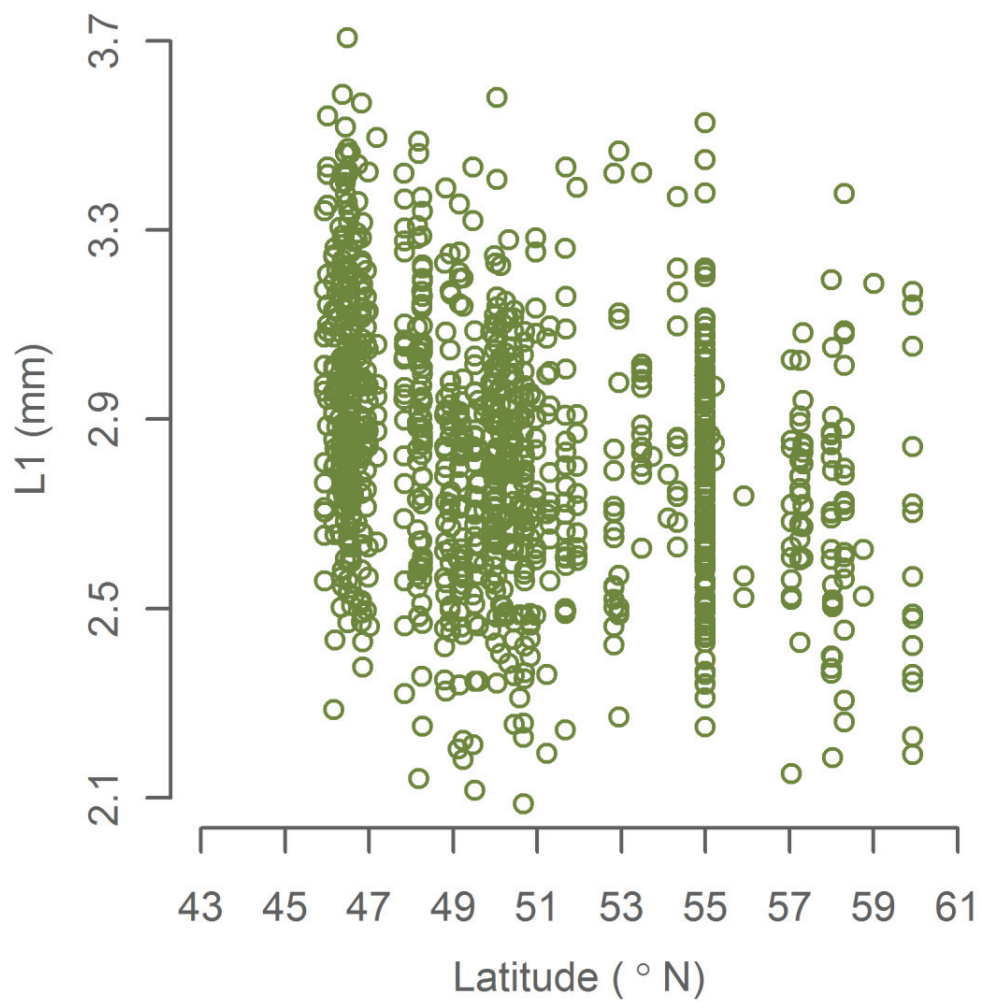


Figure S 3. L1 (otolith growth from hatch to first winter) from spawning mackerel by latitude (including 54-61°N).

Tables

Start model	Significant terms	Est.	S.E.	P
Log (Body length) ~ factor(Year) + Latitude + E/W	Intercept	3.73	0.14	<0.001
	Latitude	-0.012	0.003	<0.001
Log (L1) ~ factor(Year class) + DayOfYear + Latitude + E/W + Day : Lat interaction + E/W : YC interaction	Intercept	1.67	0.08	<0.001
	Latitude	-0.013	0.002	<0.001

Table 1. Start models and parameter estimates for final models based on the area 44-54°N.

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Appendix V

Mixing Between Mackerel (*Scomber scombrus*) Stocks in the Northern Spawning Areas

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Abstract

The perception of North Sea mackerel (*Scomber scombrus*) as an isolated natal homing stock has been prevailing in mackerel science for half a century. I reject this de-facto accepted hypothesis by demonstrating relationships between spawning in western and North Sea areas. My findings, based on unique larvae samples collected before the North Sea mackerel collapse, show that the exchange is not a recently emerged phenomenon due to the collapse. The key factor driving this part of the spawning migration dynamics is likely to be spring temperature, as the exchange is found to be strongly correlated with temperature in the current that flow NE along the shelf edge from West to North of Scotland where it enters the western North Sea through the Fair Isle channel and East of the Shetland Islands. This novel interpretation of North Sea mackerel has implications for research, assessment and management of mackerel in the North East Atlantic and it demonstrates the dynamic spatial behaviour of a species that is purely pelagic through all its life stages. The dramatic history of mackerel in the North Sea consequently needs to be reviewed by expanding the single stock assessment techniques to account for migration dynamics and exchange with other spawning areas.

Introduction

Mackerel (*Scomber scombrus*) is one of the most abundant and widely distributed migratory fish species in the North East Atlantic [1]. During the last century large changes in its abundance and distribution have been observed in several areas of the North East Atlantic especially in the North Sea [1-3]. In the North Sea mackerel was abundant and lightly fished until the late 1960s, when the development of modern sonars, power blocks and single-vessel purse seining, led to a ten-fold increase in mackerel landings [4]. The fishery in the North Sea led to a major reduction in abundance and spawning of mackerel in the North Sea in the 1970s and, despite specific fisheries regulations to protect mackerel, the biomass of spawning mackerel in the North Sea has not again increased to its former level [2]. In the last decade the biomass of spawning mackerel was 150-230 kt [1], compared to over 2 500 kt in the beginning of the 1960s. [5,6]. While several explanations for the lack of spawning mackerel in the North Sea have been suggested [2], the classic interpretations are all based on the understanding of North Sea mackerel and mackerel west of the British Isles as two separate natal homing stocks or “spawning components” (Figure 1). This is the perception of the population structure of mackerel in the North Eastern Atlantic that has persisted until today [1,7,8]. Recently a study on juvenile growth patterns demonstrated the natal homing behaviour in the NEAM population [9], providing further support to the classic view of the independent North Sea stock collapse.

A new index of North Sea mackerel spawning stock size have recently been published based on a unique historic material of mackerel larvae catches from the Continuous Plankton Recorder (CPR) survey and a new approach to CPR data modelling [2,10]. Apart from documenting the dramatic decrease, the new index also showed substantial interannual variability in the period of high abundance from early 1950s to late 1960s [2]. The interannual variation clearly exceeds the potential effects of recruitment and mortality, because mackerel does not mature before 2-3 years of age [1], and can live over 20 years [4]. Other migrating pelagic species, such as herring, are also structured into natal homing spawning stocks. These stocks are not isolated as straying between the stocks has been documented [11,12]. Similar connectivity, between the mackerel stocks in the North Sea and the western areas, is a potential explanation for the observed interannual variation of North Sea mackerel. This would, however, challenge the accepted explanation of the historic development of an isolated North Sea stock.

To test the hypothesis of mixing between the North Sea and western spawning component; I compare spawning stock sizes (proxied by densities of early larvae) in the North Sea and the Celtic sea. If the two stocks are indeed separate, then the historical development of stock sizes should most likely differ (H^1_0) and interannual variability should *not* be negatively correlated (H^2_0) as this would indicate that mackerel can switch spawning area preference from year to year. I furthermore investigate the influence of environmental conditions on the spawning migration (switching of areas) in this period.

Materials and methods

Mackerel spawning stock size index

Mackerel larvae from Continuous Plankton Recorder (CPR) surveys in 1951 to 1974 in 51-61°N, 3.5°W-9.5°E and 47-53°N, 13°W-0°E were kindly provided by SAHFOS. The CPR were towed by ships of opportunity at speeds in the range 15–20 knots and at an approximate depth of 10 m. Water entered the recorder through an aperture of 1.62 cm², and was filtered through a continuously moving band of silk with an average mesh size of 270 µm. The plankton was fixed in formalin. The silk band was divided into samples representing 10 miles of tow, equivalent to approximately 3 m³ of filtered seawater. Methods of counting and data processing are described by [13,14]. The dataset consisted of 2,870 larvae observations in 21,906 samples, widely spread through the spawning season in the North and Celtic Seas (Figure 2).

A log-gaussian cox process model [15] was used to analyse the data. It was implemented as described in [2,16] except that thermocline depth was not applied as a fixed effect as no data were available for the Celtic Sea. To test the effect of this alteration, I compared the North Sea index modelled with and without thermocline depth.

The comparison of larvae indices in the two areas were restricted to 1955-1974, because the Celtic Sea area were inadequately surveyed before 1955 and spawning in the North Sea decreased dramatically during the 1970s. H^1_0 (stock size trends not correlated) was tested by correlating 3 and 5 year running means as proxies for stock size trends. H^2_0 (interannual variability not negatively correlated) were tested on indices from the period 1958-1966. No marked trends was apparent in this period and the spawning in the North Sea was at a high level, making it more likely that fluctuations could be detected in the western area if the mackerel switched spawning area from year to year. This combination makes the period from the change in CPR methodology (1958) to the initiation of the Norwegian purse seine fishery (~1966) ideal for testing H^2_0 . However, due to the low number of observations in this period (9 years), H^2_0 was also tested by correlating detrended annual index values, calculated as 3-year running means minus the annual value. This was done for the whole period 1955-1974.

I furthermore tested if environmental parameters important for adults, eggs and larvae could have driven the migration in the period where spawning and the signal-to-noise ratio in the larvae index were at its heights. This study period were exploratively expanded to 1951-1966, which corresponds to the period from the beginning of the Dutch fishery (> 10 kt / year) to the beginning of the Norwegian overfishing (> 500 kt / year).

A multivariate linear model was built to explore potential causes for the long term temporal variability in spawning in the North Sea. The North Sea larvae index as provided by [2] was

again used as proxy for annual spawning intensity. The starting model included the following candidate predictors:

- Sea surface temperature (SST) in the spawning area and early season, because SST has been shown to be correlated with spawning distribution in the western areas [17].
- Winter temperature in the shelf edge current where mackerel overwinter, because this affects the distribution prior to the spawning migration with a possible knock-on effect into the spawning season [3].
- Sea surface salinity (SSS), because salinity has been shown to be related to spawning in a more coarse long term analysis of larvae abundance. This relation may not be causal, but salinity could indicate certain water masses that are preferred by mackerel [10].
- Zooplankton concentration in the whole North Sea, as this is important food for larvae, juveniles and adults [18].

Interactions were omitted due to the limited number of data points. For the same reason; I also tested for correlation between the response variable and each single predictor variable separately. Predictor variables were Z-transformed. The *corvif* function of the AED R-package was used to calculate Variance Inflation Factors (VIF). VIFs are indicators of collinearity. The predictor variables were sufficiently independent to be used in the same model fit, if the VIFs were > 3 [19]. Inspection of Auto Correlation Function (ACF) plots (not shown) revealed no temporal autocorrelation of the response variable. Model-building was done “backwards” by sequentially removing insignificant ($p > 0.05$) terms.

The analysis of potential environmental effects was further expanded in the spatial domain. This was done, for the parameters that were found to be significant in the first model, by calculating time series for smaller areas ($2^\circ \times 4^\circ$ rectangles) and mapping each areas correlation with the larvae index.

Temperature, salinity and zooplankton

Temperature and salinity time series representing the conditions prior to and during spawning in surface waters in spring was calculated. Yearly values of SST and SSS were estimated as the average of monthly SST and SSS in April-June in the area $56-62^\circ\text{N}$, $0-4^\circ\text{W}$ and in $2^\circ \times 4^\circ$ rectangles. Observations originated from depths of $< 10\text{m}$ from CTD/bottles/underway/pump/moorings and were obtained from ICES hydrographic database [20].

The second temperature time series represented the conditions experienced by mackerel through winter as it migrates in the continental shelf edge current, that flow into the western edge of the Norwegian trench (Figure 1 and Figure 1-2 in [3]). Mackerel distribution during winter is known to be related to the temperature in this current, possibly with a propagating effect on spawning [3]. Details of this temperature time series have previously been published [3].

Zooplankton data from CPR surveys from 1958 to 1974 were obtained from the SAHFOS database as abundance by species by sample. Data from 1948-1957 were not available by species. Biomass by sample was calculated using the mean dry weight by species from [21]. Mean zooplankton concentration (g/m^3) by year were calculated as a simple average of all samples in the North Sea ($50\text{-}60^\circ\text{N}$ 4°W - 8°E) in the peak spawning season (June). Biomass was used instead of abundance because mackerel in all life stages are size selective feeders and prefer larger calanoid copepods over smaller cyclopoid copepods [22-26]. The CPR is known to under-sample in some situations. I did not correct for under-sampling because it mostly affects smaller species [21].

Modelling and correlation tests were performed in R version 2.12.1 with the “stats”, “nlme”, and “sp” packages [27]. Correlation test results were adjusted for the effects of temporal autocorrelation as described in [28].

Results

Removal of thermocline depth from the original larvae model [2] did not affect the *temporal* aspect of the larvae model as I found the indices modelled with and without thermocline depth highly correlated ($p < 0.001$, $R^2 = 0.996$).

The running means (rm) of larvae indices in the North and Celtic seas were significantly positively correlated (3 year rm: $R^2 = 0.38$, $p = 0.007$, Figure 3; 5 year rm: $R^2 = 0.33$, $p = 0.019$). H^1_0 was therefore rejected.

The detrended larvae index in the North Sea 1955-74 were negatively correlated with the larvae index in the Celtic Sea ($R^2 = 0.23$, $p = 0.046$) and so were the indices for the period 1958-1966 ($R^2 = 0.78$, $p = 0.004$, Figure 4 middle). I consequently rejected H^2_0 . The substantial interannual variability in this period 1958-1966 was higher in the North Sea ($\text{CV} = 56\%$) than in the Celtic Sea ($\text{CV} = 27\%$).

The only significant term in the final model of mackerel larvae in the period 1951-1966 were the SST in April-June ($R^2 = 0.65$, $p < 0.001$, $56\text{-}62^\circ\text{N}$, $0\text{-}4^\circ\text{E}$, Figure 5). Maps of spatial correlation patterns between the index and SST in spring (Figure 6) showed strong correlations in the current that flow NE along the shelf edge from West to North of Scotland where it enters the North Sea through the Fair Isle channel and East of the Shetland Islands. Comparable strong correlations were also found in this current as it continues SE along the Scottish East coast inside the North Sea. Weaker, but still significant, correlations were found in the central North Sea and Dogger area. SST in the Eastern North Sea, South of Dogger, the English Channel and the Celtic Sea were not significantly correlated to the larvae index.

Discussion

My analyses have demonstrated relationships between spawning in the North Sea and the western spawning area. Positively correlated long term trends and negatively correlated interannual variation indicates that the two spawning populations are connected. I consequently reject the null-hypothesis of reproductively isolated natal homing stocks and accept the alternative hypothesis of connected *contingents*.

While interannual variation dominated the spawning variability in the North Sea in the period 1958-1966 (CV=56%), it was of less importance for spawning in the Celtic Sea (CV=27%). This suggests that the part of the population that migrated northwards into the North Sea in these years was a larger part of the mackerel that spawned in the North Sea than in the Celtic Sea, i.e. on average more mackerel spawned in the Celtic Sea than in the North Sea.

The presented interpretations of my results are under the assumption that the larvae index is a valid index of spawning mackerel. Alternative explanations of the observed fluctuations in the 1950s and 1960s can be imagined, such as variation in mortality in the short egg-larvae phase, and/or catchability due to changes in vertical distribution. If mortality and/or catchability had fluctuated inversely between the North and Celtic Seas in a non-random way, then this should have been due to a common factor with adverse effects in the two areas. I found temperature to be highly correlated with the index, so this would be the prime candidate for alternative explanations. However, mortality and catchability are *local* phenomena, which can be expected to respond to *local* environmental conditions. Since neither the larvae index in the North Sea nor in the Celtic Sea were related to temperatures in the Celtic Sea (Figure 6 and S1), I do not find it likely that these processes caused the observed patterns. Furthermore, if the pattern was caused by CPR catchability changes due to some large scale physical feature, then I would expect to find the same pattern in the CPR time series for other species. No significant correlations were found between abundance time series of mackerel larvae and larvae of Horse mackerel, Clupeids, Gobies, Sandeels or Dragonets (Unpublished data). Finally, I found that thermocline depth, that likely affects larvae catchability, only affected the spatial dimension of the index *not* the interannual variation. It is also worth noting, that the water immediately behind a large, fast-moving vessel is likely to be mixed and homogenized well below the CPR towing depth [13].

The hypothesis of North Sea mackerel as an isolated natal homing stock has been prevailing in mackerel science for half a century. My rejection of this hypothesis has implications for research, assessment and management of mackerel in the North East Atlantic. One consequence is that the dramatic history of the mackerel in the North Sea needs to be reviewed by expanding the single stock assessment techniques to account for migration dynamics and exchange with other spawning areas.

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Figures

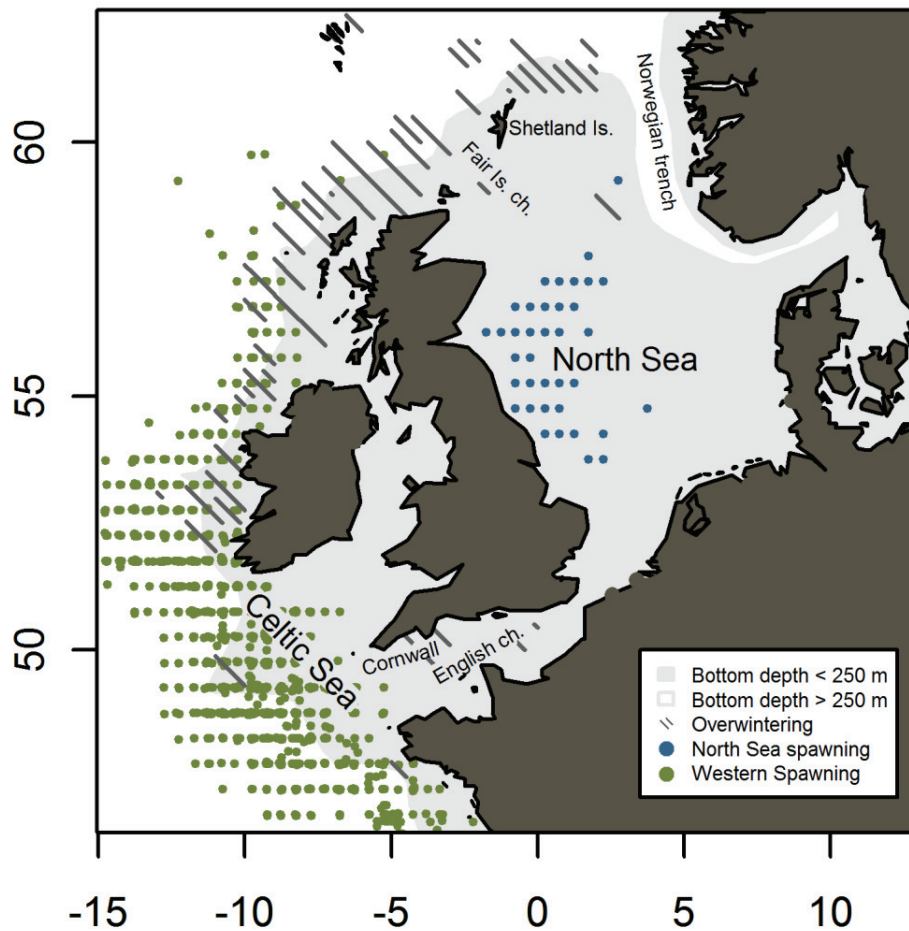


Figure 1. Mackerel populations and distribution around the North-west European shelf. Continental shelf marked in grey (bottom depth < 250 m). Spawning areas indicated by dots. Each dot marks an observation of $50+ \text{ eggs m}^{-2} \text{ day}^{-1}$ (data from international mackerel egg surveys in the North Sea 2002-2011 [6,29,30] and western areas 1977-2007 (ICES WGMEGS)). Stripes mark the distribution of mackerel before spawning (based on commercial catch data in January-March 1985-2010) [3].

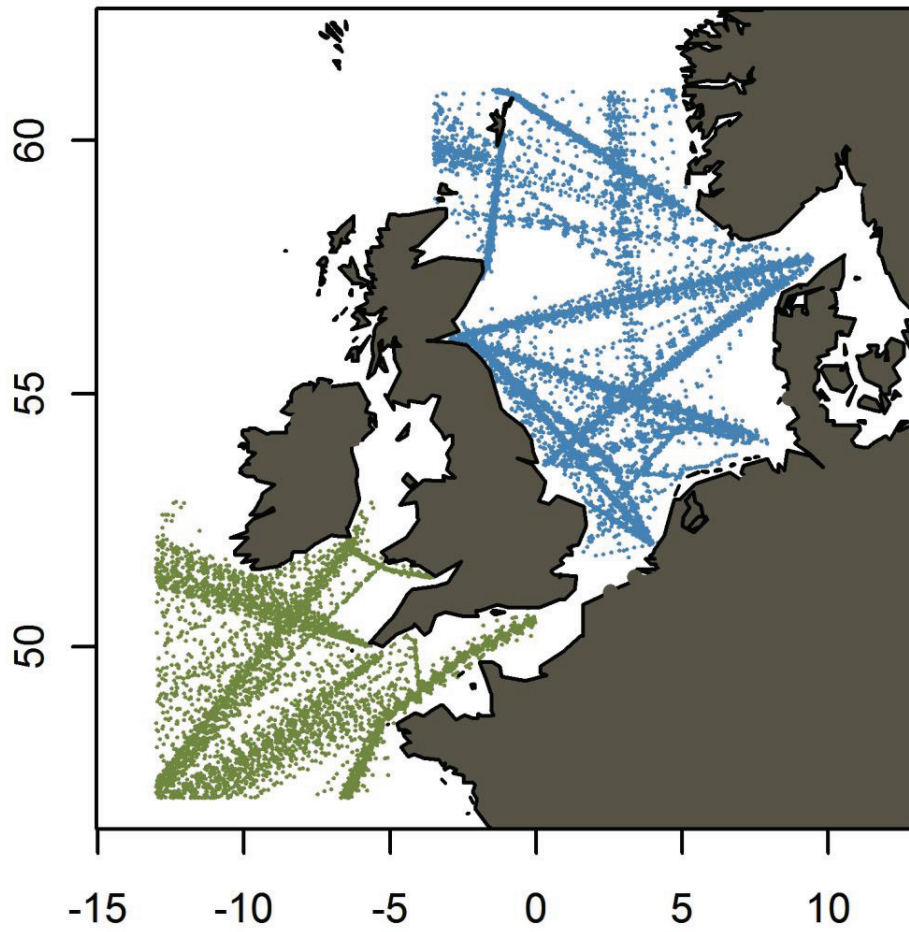


Figure 2. Continuous plankton recorder samples from 1955-1974 in the studied areas.

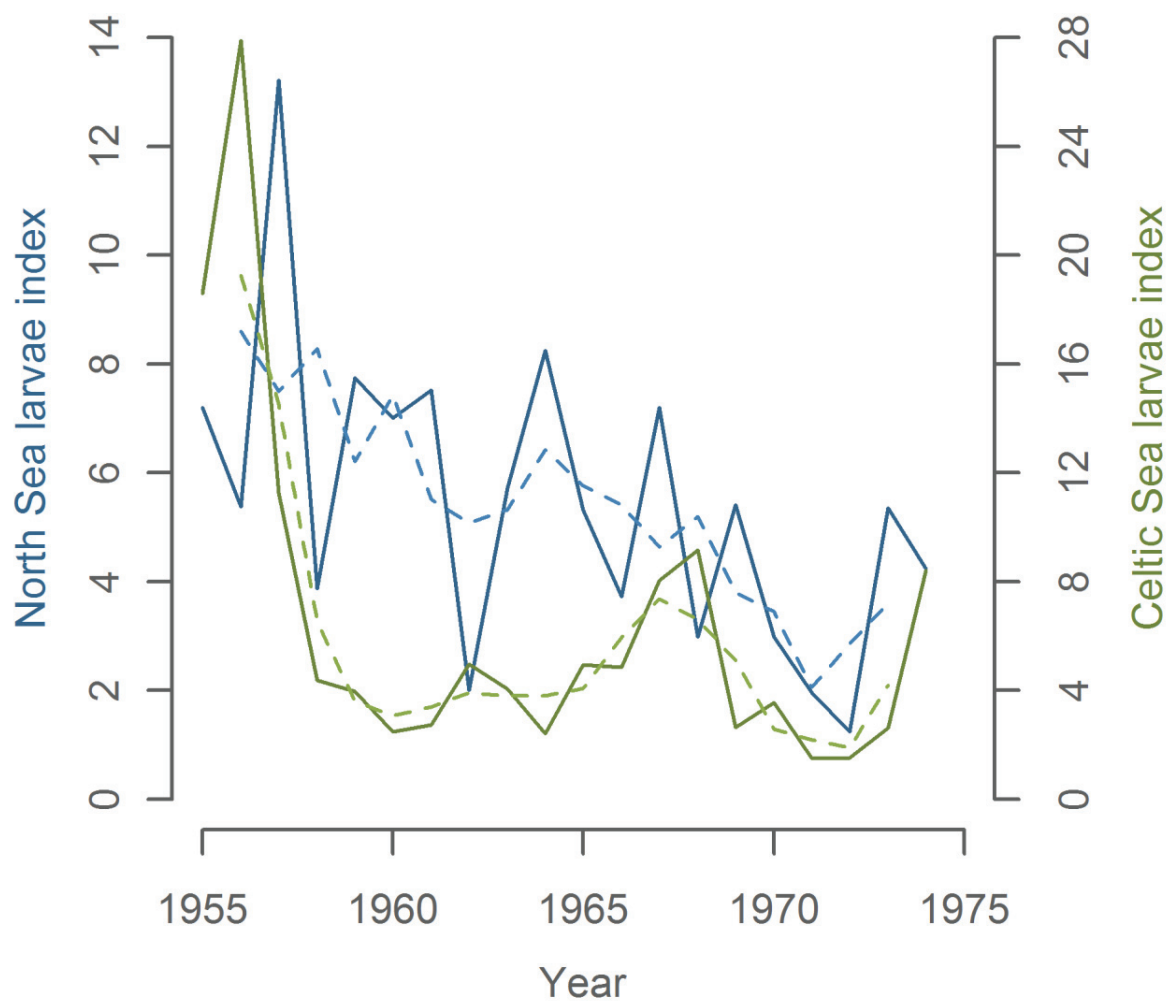


Figure 3. Mackerel larvae indices in the North and Celtic Seas (full lines) with 3 year running mean trend lines (dashed lines).

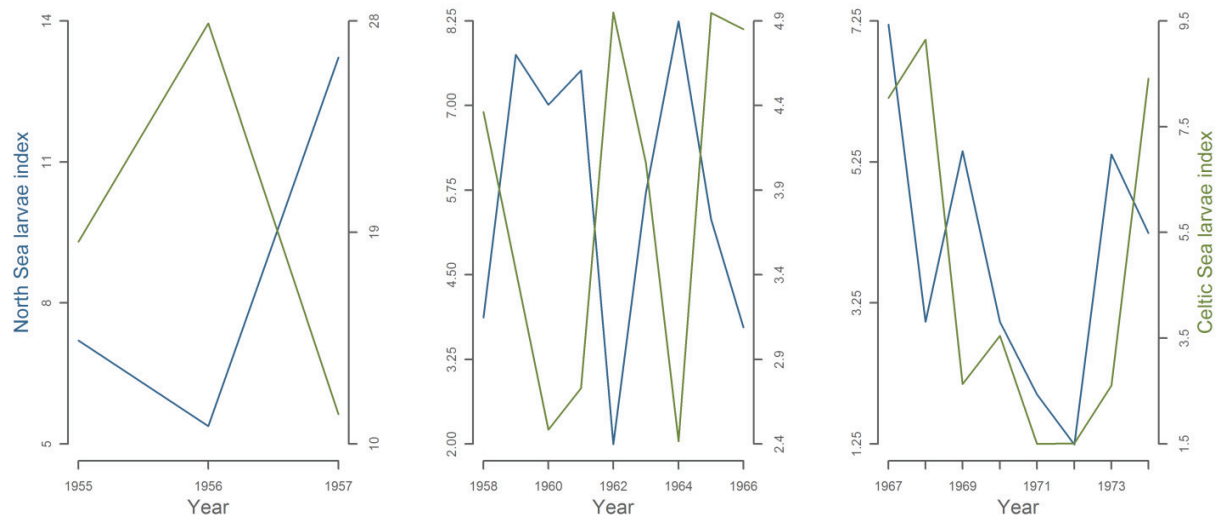


Figure 4. Mackerel larvae indices in the North and Celtic Seas broken into three periods.

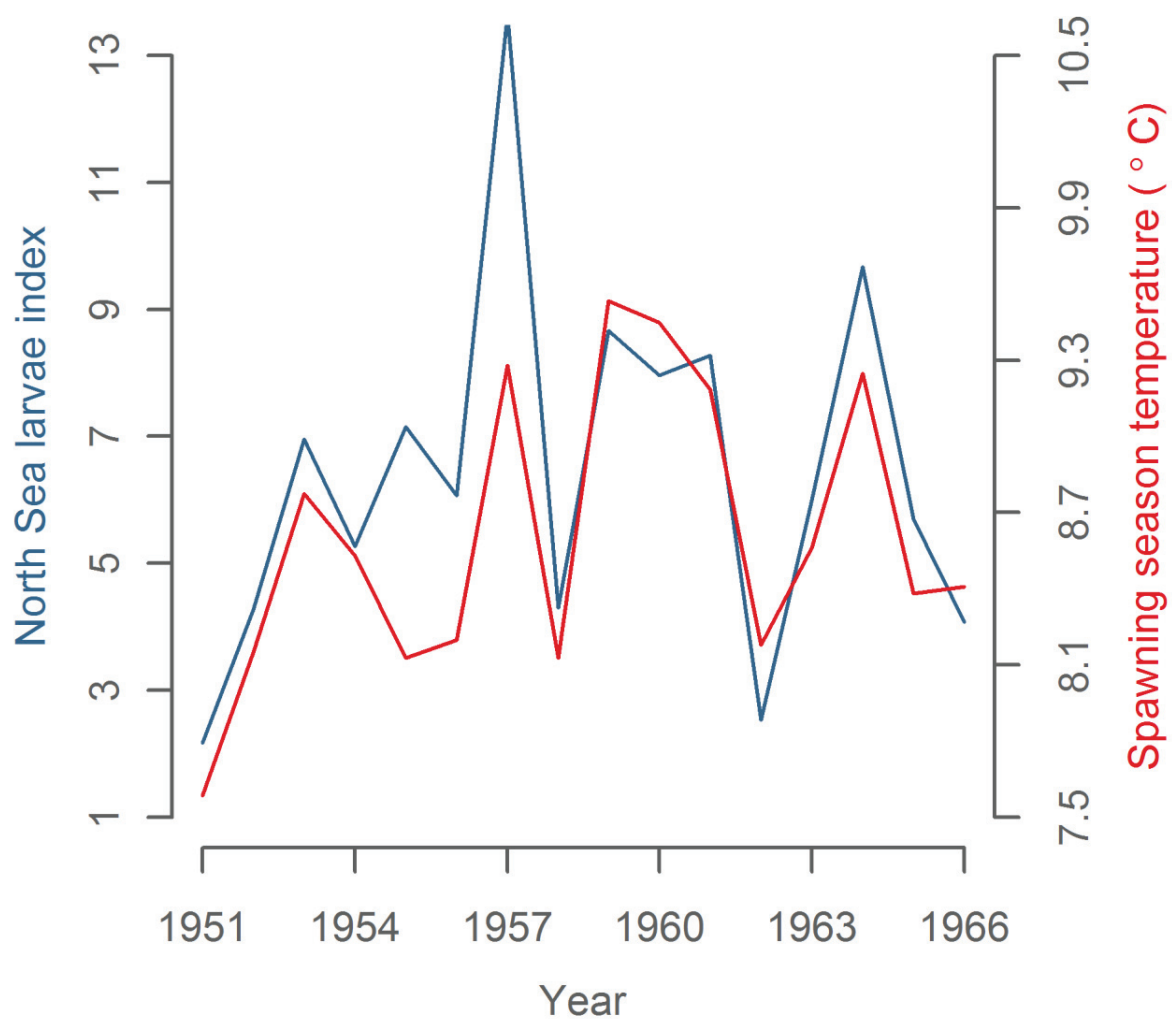


Figure 5. Mackerel larvae index from CPR surveys in the North Sea and sea surface temperature in the early spawning season (April-June) in the north-western North Sea (56-62°N, 0-4°W).

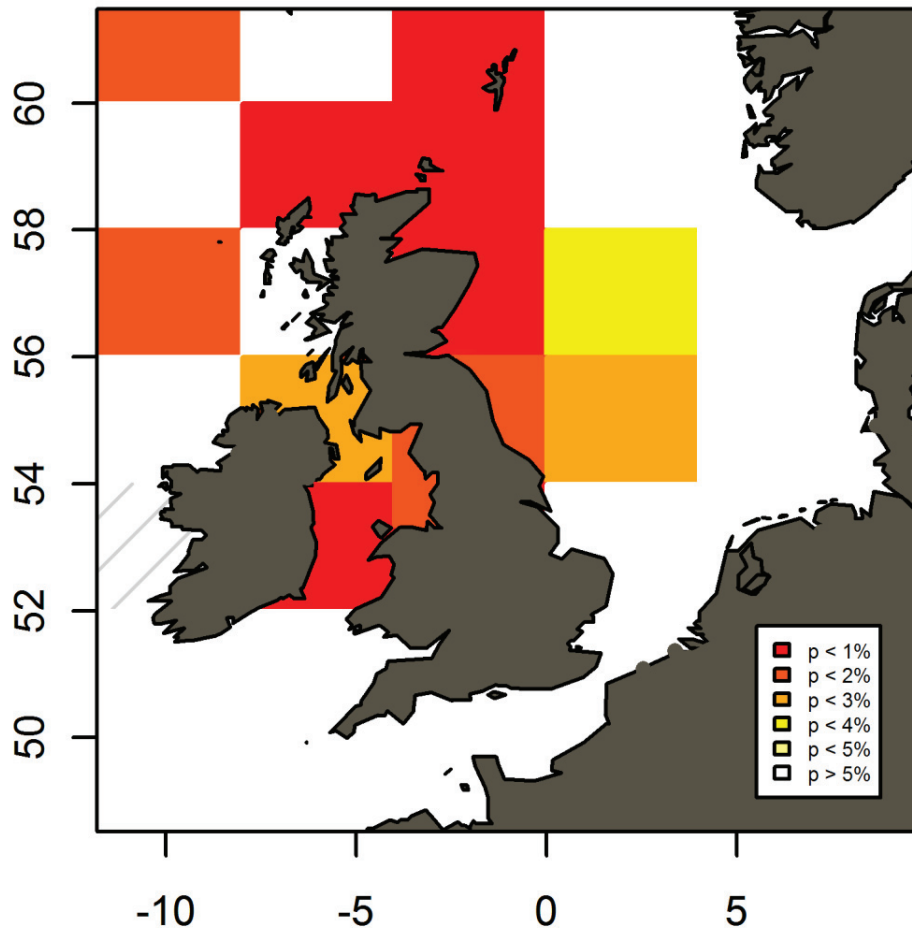


Figure 6. Spatial correlation patterns between the mackerel larvae index from CPR surveys in the North Sea and sea surface temperature in April-June. Stripes indicate areas with insufficient temperature observations (< 6 years).

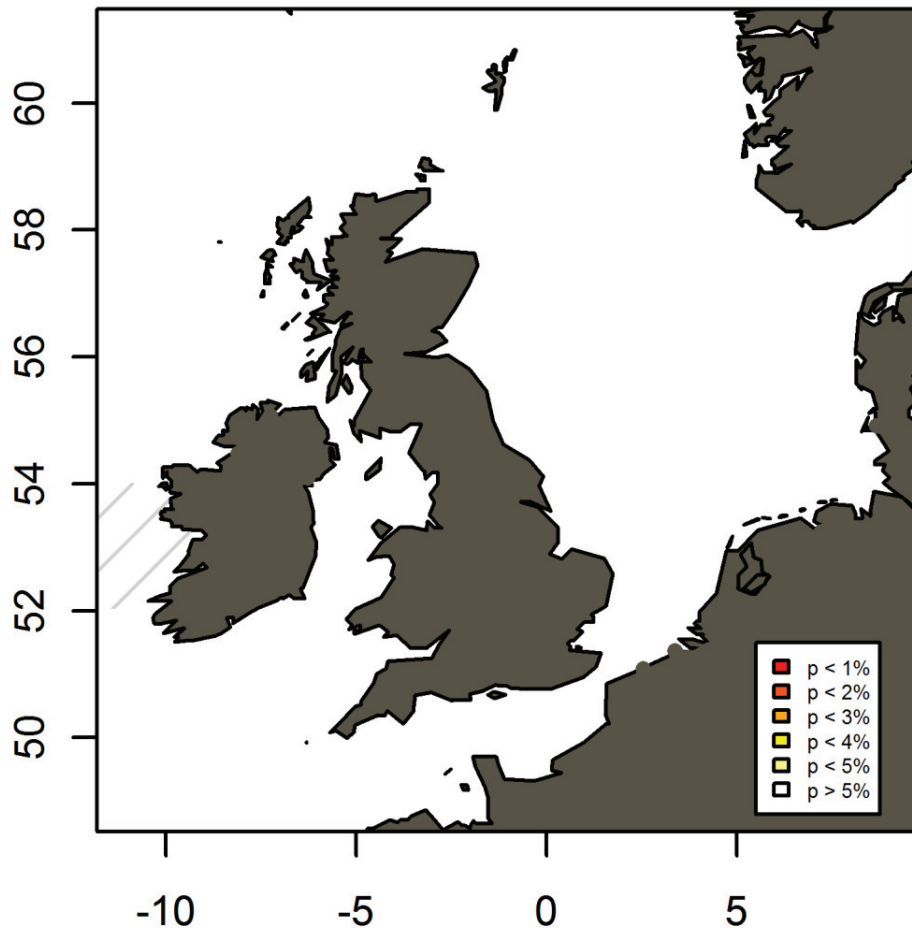


Figure S1. Spatial correlation patterns between the mackerel larvae index from CPR surveys in the Celtic Sea and sea surface temperature in April-June. Stripes indicate areas with insufficient temperature observations (< 6 years).

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Appendix VI

Population structure and spatial spawning dynamics of Atlantic Mackerel (*Scomber scombrus*)

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Abstract

Large changes in mackerel (*Scomber scombrus*) abundance and distribution have been observed in the North Atlantic. Key aspects of the population structure and environmental and anthropogenic drivers of the spawning dynamics are reviewed.

Mackerel clearly displays isolated and different life-cycle patterns across the Atlantic Ocean. On each side, there seem to be a complex of spatiotemporal diversity, but it is not evident that they divide further into more closed life cycle patterns i.e. contingents. It appears that a dynamic interplay between natal homing and substantial straying, result in a more complex structure than what is reflected in the traditional separation into spawning components. On this basis, I suggest that the mackerel population in the North East Atlantic is better described as a dynamic cline, rather than connected entities. Hydrography and mackerel behavior may then affect the steepness of the gradient at various locations within the cline as these features vary for each generation.

A simple outline of this model was then used to investigate the most dramatic change in mackerel history, namely the collapse of the mackerel in the North Sea in the 1970s. I found that the traditional explanation of the collapse seems to have overlooked a range of unfavourable environmental changes that likely added to the effect of high fishing pressure. I did not find indications for any irreversible genetic or behavioral loss caused by the collapse. The previously unexplained lack of rebuilding of spawning in the North Sea consequently seemed related to two environmental factors that have remained unfavorable, namely wind induced turbulence and zooplankton concentration. Furthermore, the large commercial autumn-winter fishery in the North Sea continues to land unknown quantities of mackerel with an affinity for spawning in the North Sea.

In the North East Atlantic spawning has recently increased in the main western spawning areas and expanded into new areas towards north-west. Since the surface water in the new north-western area recently became warmer than what appeared to be critical for the historic northern spawning migration into the North Sea, it can be concluded that with regards to temperature, these areas have become favourable as a mackerel spawning habitats.

Conservation of genetic and behavioral biodiversity should be of concern when managing mackerel fisheries. However, the mackerel seems less prone to unbalanced exploitation than many other commercial species.

Introduction

Mackerel (*Scomber scombrus*) is one of the most abundant and widely distributed migratory pelagic fish species in the North East Atlantic where it is caught by a large pelagic fishery with annual landings between 500 and 1000 thousand tonnes [1]. During the last century large changes in abundance and distribution have been observed in the northern parts of its distribution area - especially in the North Sea [1-3]. The reason for these changes have been widely discussed, but are poorly understood [1]. Large changes in mackerel abundance and distribution have significant ecological and economic impacts. The political and direct economic impacts are easily observed and well known [4,5]. The ecological impacts are more difficult to observe, but include altered predation pressures on zooplankton and pelagic larval and juvenile stages of fish, including a number of commercially important fish stocks. The ecological and economic importance of these changes are likely to be large, but have not so far been assessed [6]. The aim of the present review is to investigate the relationship between the distribution of spawning mackerel in the northern areas and the underlying environmental and anthropogenic drivers. The spatial population structure of mackerel has been the subject of repeated studies over the last 100 years of mackerel science [7,8] and a review of these studies is the first step towards a new understanding of the drivers of mackerel distribution. Existing literature is supplemented with demographic data, and used to develop a conceptual model of the spawning biomass fluctuations in the North Sea. With this model, I proceed to investigate the collapse of the North Sea mackerel, and draw parallels between the historic development and the recent expansion.

Spatiotemporal life cycle patterns of the Atlantic mackerel

Traditional spawning components

Mackerel live their entire life in the pelagic. Early life stages (eggs and young larvae) drift passively with the currents until they start vertical migration and eventually horizontal migration as young juveniles. When mature, most mackerel perform extensive migrations outside the spawning season. In the North East Atlantic (NEA) mackerel spawn from the Mediterranean Sea in south to the Faroe Islands in the North and Hatton bank in the West to Kattegat in the East. Spawning starts in February off the Portuguese coasts and ends in July north of Scotland and in the North Sea (Figure 1) [9]. While spawning vary locally from day to day [10,11], it seems to form one large spatiotemporal continuum on the larger scale. However, relatively low levels of

spawning in the English and Fair Isle channels separates the main spawning areas in the North Sea from the western areas along the continental shelf edge [12]. Despite the lack of complete spatial or temporal separation, NEA mackerel have traditionally been divided into three distinct entities, namely the Southern, western and North Sea spawning component (Figure 1), [1,13]. In the North West Atlantic (NWA) mackerel spawning have not been mapped by synoptic surveys. The mackerel are fished from North Carolina in the South to Newfoundland and Labrador in the North [14]. Sette (1950) suggested the presence of two entities of mackerel in the NWA, namely a southern and a northern contingent spawning off the US and Canadian coasts respectively [14,15].

Despite numerous studies, there is still very limited knowledge on the isolation and mixing between these 5 entities (here called spawning components) and they remain weakly defined. Populations where life cycle diversities are categorized into multiple components or contingents are often referred to as a *metapopulations* [16]. No previous study has discussed if the term metapopulation is appropriate for the Atlantic mackerel.

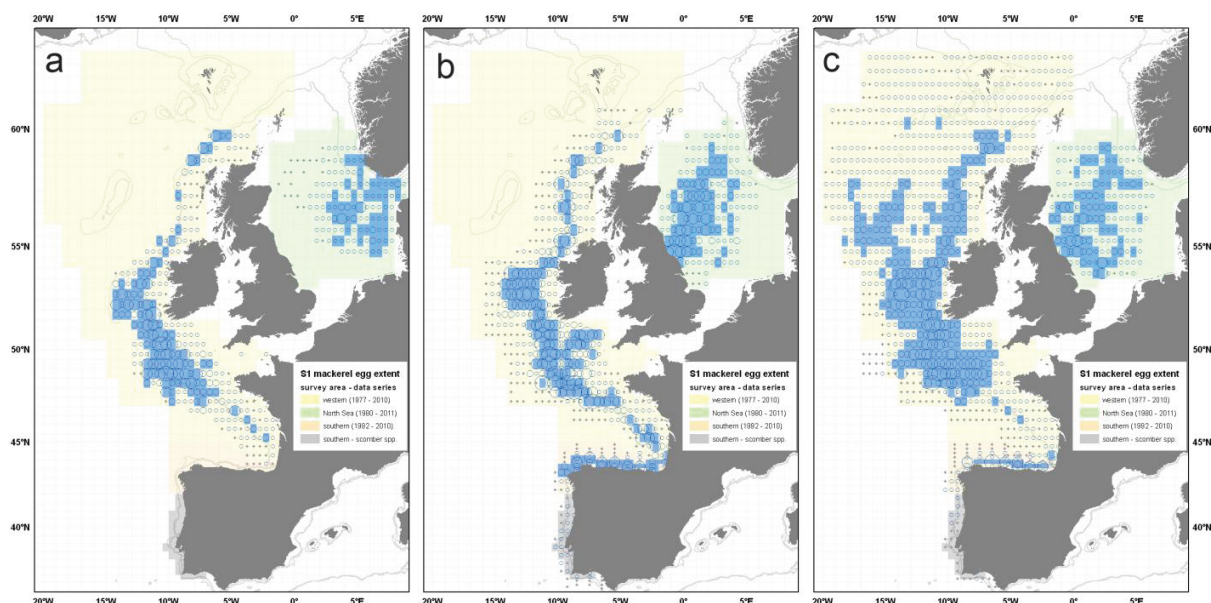


Figure 1. Spawning area of North East Atlantic mackerel. Maps show mean egg production (stage 1 eggs $\text{m}^{-2} \text{day}^{-1}$) by half ICES rectangle for all stations sampled during the international mackerel egg surveys in 1986 (a), 2004-2005 (b) and 2010-2011 (c). Circles are square root scaled to the maximum value in any one half rectangle for the given year and survey area (West/South or North Sea). Crosses denote locations where sampling was undertaken but where no spawning was recorded. Area capturing 90% of spawning within that area/year is marked in blue. Maps by Finlay Burns (Marine Scotland).

Contingents and metapopulations

A life-cycle pattern can be defined by recurring and persistent migration and dispersion processes that link the sequential habitats used by the different life stages [17]. A population can then be characterized by a single pattern i.e. Panmixia, or a diversity of patterns i.e. a metapopulation consisting of multiple contingents. While panmixia is simple to define as “random mating within the population” (www.Wikipedia.org), it is more challenging with the metapopulation concept. Levins first defined the metapopulation as: *a population of local populations which were established by colonists, survive for a while, send out migrants, and eventually disappear. The persistence of a species in a region depends on the rate of colonization successfully balancing the local extinction rate* [18]. [19] later relaxed the definition to its most simple form: *presence of discrete local breeding populations connected in exchange of individuals*. [16] revised the numerous definitions and usages and found that the concept were being increasingly used, but also misused. They underlined the importance of contingents having nontrivial probabilities of experiencing extinction during the lifespan of the metapopulation.

Large marine fish stocks, like cod and herring, consist of a diversity of life-cycle patterns. They are thus often referred to as metapopulations consisting of contingents. The life cycles are usually contained within persistent oceanographic structures that ensure larval retention and/or control migration of adults [20]. However, the contingents can be more or less connected by straying of individuals through dispersal in the larval, juvenile, and/or adult phase [20,21]. Life-cycle patterns are not necessarily genetically inherited and their persistence could be explained by phenotypic plasticity and social behavior [17,22]. The differences in life-cycle patterns are often reflected in phenotypic characters [20] due to the different environmental conditions that each contingent experience. In some cases, low contingent connectivity on an evolutionary time scale, have allowed for minor genetic differentiation [23,24]. Some authors have argued that species like cod, does not form true metapopulations because the extinction-criteria are not likely fulfilled for these species due to the high mixing (straying) rates [16]. I disagree with this statement. All species that are found on both sides of the Northern Atlantic, and where fish from each side do not interbreed, could become extinct on either side of the Atlantic. Subsequent recolonization could then take place in warmer times, where the two sides are not isolated by cold water masses.

Key questions regarding metapopulations and contingent connectivity are: Are there more than one closed life-cycle pattern, i.e. contingents? Is there a possibility of extinction of at least one contingent? Are there strays that switch from one life cycle to another? Does the breeding success of stray mackerel counter the isolating effect of natal homing, leading to a prevention of genetic differentiation?

Phenotypic plasticity, homing and genetic diversity

Most attempts for phenotypic classification and identification of mackerel spawning components have failed. Some studies on characteristics such as juvenile growth patterns in otoliths [25,26], age compositions [27], length at age [27], protein polymorphism [28,29], nematode (*Anisakis simplex*) [27] and tapeworm (*Grillotia smaragdina*) infection rates [30] were based on individuals from the respective spawning areas that were *not* all in the process of spawning (*i.e.* ripe/running). These studies may have included mackerel from several discrete components, due to the swimming capabilities of mackerel. One fish was marked in the channel off the South-East coast of England and recaptured 1200 nm away off Shetlands after just 13 days [31]. As mackerel swim continuously day and night [32], this corresponds to approximately 2 knots, which is well below the maximum swimming speed measured in-situ on schools [33]. After spawning, some mackerel from the south-western areas of the NEA, migrate into the North Sea before spawning in the North Sea has ceased [34]. Consequently, conclusions on natal homing and the existence of multiple components cannot be drawn from these studies. Other studies were correctly based on spawning individuals, but found no difference in ectoparasite infections [35] or blood phenotypes [36]. Otolith shape do not differ significantly among the NEA components (Jansen unpubl. analysis of 652 mackerel otoliths), but it does in the NWA and across the Atlantic [37]. However, the distributions of shape parameters were only sufficiently discrete in the cross-Atlantic comparison for actual identification purposes (60-87% successfully identified) [37]. Most recently, significant differences in juvenile growth patterns have been detected *within* the western component in the East Atlantic [38]. The latter study compared growth data (fish length) with latitude and found that that southern juvenile mackerel attained a greater length than those from further north. Examination of juvenile otolith rings on adult spawning mackerel showed a similar significant relationship between growth and latitude for adult mackerel spawning between latitudes 44°N (Bay of Biscay) and 54°N (west of Ireland). This means that a significant proportion of a given year class returned to spawn at higher latitudes, than other individuals from the same year class that were hatched at lower latitudes. These findings thus rejected panmixia by indicating a type of natal homing behaviour among North East Atlantic mackerel [38]. The authors were unable to distinguish between absolute spatial homing (*e.g.* as with salmon) and *inter-cohort relative natal homing* (spatial natal homing relative to other individuals from the same years class), as the observed growth patterns could appear while the entire mackerel population moved north-south from year to year due to variable environmental conditions. Mackerel is a serial batch spawner that potentially could migrate far between the spawning of each batch. This spatial aspect of the mackerels spawning behavior has not been studied and remains a serious lack of knowledge for the analysis of homing.

Tagging data strongly support the cross-Atlantic separation. Out of the approximately 1 million mackerel tagged in the East Atlantic, none have been reported as recaptured in the western Atlantic [7,34,39]. These experiments have unfortunately not been designed to follow the homing and mixing of different putative components as the maturity stage has not been recorded

during tagging and recapture. However, incomplete mixing between mackerel tagged in the Celtic Sea during spawning time and mackerel tagged in the North Sea in August after the spawning season (i.e. a mixture of migrants) [40], support rather than reject some sort of separation.

The cross-Atlantic separation had led to genetic differentiation on mitochondrial DNA [41]. Whether the balance between homing and mixing has allowed for genetic differentiation within the populations on each side of the Atlantic remains to be thoroughly examined. Three studies of gene variants did *not* find that the samples from the NEA grouped into the expected clades (spawning components) [28,41] and (Pers.Comm. Frode Lingaas, 21 Sept. 2011). However, a different statistical analysis of the mitochondrial DNA allele frequencies from one of the studies separated the 3 samples from the western area from the rest in the NEA [41]. However, this analysis was based on relatively few samples (3+3+4) with few individuals (22+17+16) and it did not account for differences between year classes. The weak, support for genetic differentiation in this study, may therefore have been on an ecological time scale rather than on an evolutionary time scale. Genetic studies on the mackerel in the NWA are similarly inconclusive [14]; while genetic differences have been suggested by studies on the polymorphism of some proteins [42-44], more recent phylogenetic and molecular variance analysis did not reveal genetic differences between the northern and southern components [45]. In conclusion, Atlantic mackerel clearly displays isolated and different life-cycle pattern across the Atlantic Ocean. On each side, there seem to be a diversity of spatiotemporal life cycle patterns, but no method has successfully been able to unequivocally identify the origin of spawning mackerel from any of the traditional spawning components. The tendency for natal homing within one component, does on the other hand demonstrate that mackerel exhibit the necessary behavioral element that act towards closure of spatiotemporal life cycle patterns on a more localized scale.

Mixing of components through straying

Assuming that the tendency for homing, albeit of unknown precision, is a global mackerel phenomenon; we can direct our focus on mixing processes that counter the differentiating effect of homing. Mixing can occur in all life stages and be caused by passive drift or active migration. The previously mentioned study that demonstrated homing in the western component did not find any evidence (relation to latitude) north of Porcupine bank. The lack of homing signal in the data may be due to meridional mixing during the larval drift phase in this more energetic northern area of strong meridional currents. In a study of spawning migration of adult mackerel in the northern parts of the NEA, temperature seemed to influence the choice between the Celtic and the North Sea spawning areas around 1950-1970 [46], i.e. between the western and the North Sea components spawning areas. Rather than a complete switch between the Celtic and the North Sea, mixing could have occurred along a gradient from the North Sea, west of Scotland and into the Celtic Sea as spawning expanded/retracted along the gradient in warm/cold years. Further

support of homing and straying in the adult phase may be found using natural tracers such as demographic data. Here I explore age distributions in commercial catches.

Demographic data can be used as natural tracers if the components contain strong and contrasting year classes. Mackerel recruitment in the North East Atlantic seems to be dominated by strong year classes in some periods such as the 1950s-1960s in the North Sea [47,48], early 1980s and in the latter decade [1]. From mid 1980s to 2000, recruitment seemed to be rather constant [1]. Age distributions may therefore serve as natural tracers of mackerel in some periods.

During bottom trawl surveys in the winter 1969-1970, unusual high numbers of juveniles were caught in the central North Sea, indicating massive recruitment inside the North Sea in 1969 [49]. 1969 was the last of the large year classes in the 1960s (Figure 2a). Mackerel from this year class appeared in relatively large numbers in commercial catches all through the 1970s [50,51]. To the north-west of Scotland, this strong year class was significant or dominant in the catches from March to May (Figure 2b). Later in summer the fraction of the catch belonging to the 1969 year class was much reduced, indicating that mackerel from the North Sea had either left the area and/or mackerel with another age distribution had entered. This was interpreted as evidence for multiple stocks with different age compositions [50]. However, the relative decline of the dominance of the 1969 year class could also be explained by immigration of recruit spawners that spawn later than repeat spawners [52-54] and juveniles. This explanation cannot be ruled out because the complete age distributions were not published. However, it is more insightful to consider the fraction of the catch consisting of the 1969 year class in June, where it dominated in 3 out of 5 years. In these years mackerel from 1969 were relatively old and large repeat spawners of 5-10 years of age. Large repeat spawners are known to spawn early in the spawning season [52-54]. Spawning in the North Sea begin in May, peaks in late June or early July and cease during July [55,56]. Catch data from June 1974, 1976 and 1979 therefore suggests that mackerel originating from the North Sea was spawning outside the North Sea. This supports the mixing hypothesis that previously was only supported by analysis of larval data [46].

Age distributions in more recent commercial catches have not been published with a comparable spatio-temporal resolution. However, the more aggregated age distributions printed in the yearly assessment reports from ICES can be inspected for similar patterns. Three exceptionally strong year classes have entered the northeast Atlantic mackerel population during the last decade, namely in 2002, 2005 and 2006 [1]. As with the 1969 year class, these year classes are represented in the commercial catches in exceptionally high numbers in most years. This is apparent when inspecting catches from the main feeding season, when mixing between different components is assumed to be at its height (table 2.4.1.1 in [1] and bold line on Figure 2c). Since there are no substantial fisheries that target mackerel during spawning (table 2.4.1.1 in [1]), it is only possible to compare data from different areas just prior to spawning. Age distributions of the catch in January - March from the Bay of Biscay in the south to the North Sea and waters around Scotland in the north, all have similar age compositions as the summer fisheries (Figure 2c). Juveniles, at the age of zero, are caught in bottom trawl surveys from Gibraltar to North of

Scotland. However, the main catches no so dispersed. While the primary spatial origins, of the 2006 year class, appeared to be both in the Northern part of the Bay of Biscay and west of Ireland, the 2005 year class were primarily caught in the areas between Ireland and the Outer Hebrides (Figure 3). This indicates that the strong recruitment in 2005 were a local phenomenon. Later, as adults, these mackerel was caught throughout the NEA distribution area in the months prior to spawning. The demographic data thus suggests the phenomenon known as “twinning”, Twinning is a result of substantial straying of individuals from the strong year classes and it is well-known for other species like herring [20]. Mackerel can migrate far in the time span between the commercial fisheries and the onset of spawning. However, since the spatial origin of the mackerel from the 2005 year class is very close to the main wintering areas [3], they would not be expected to pass through the Bay of Biscay. Since the 2005 year class was dominating the catches throughout the Bay of Biscay in January to March 2010, I conclude that this demonstrate “twinning” i.e. substantial straying of this strong year class.

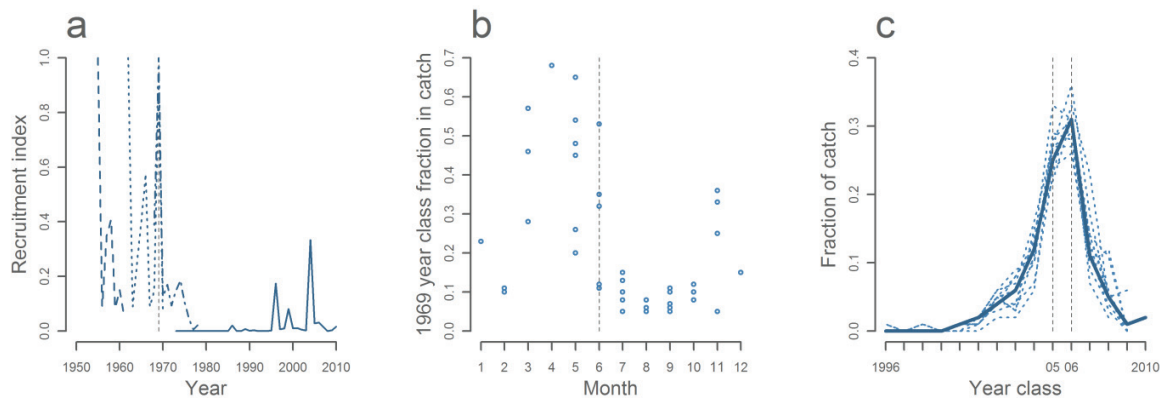


Figure 2. (a) Time series of recruitment in the North Sea indicating strong year classes. Please note that time series are not in scale. Data sources described in Appendix I. (b) Percentage of 1969 year class by month in 1974-1979 from Outer Hebrides and Cape Butt areas, data from [50]. (c) Age distributions in commercial catches in Jan-Mar 2010 by ICES division (stippled lines) and for all areas combined in Jul-Sep (bold line). Divisions with insignificant fisheries (>500,000 mackerel) in Jan-Mar have been excluded. Data from [1].

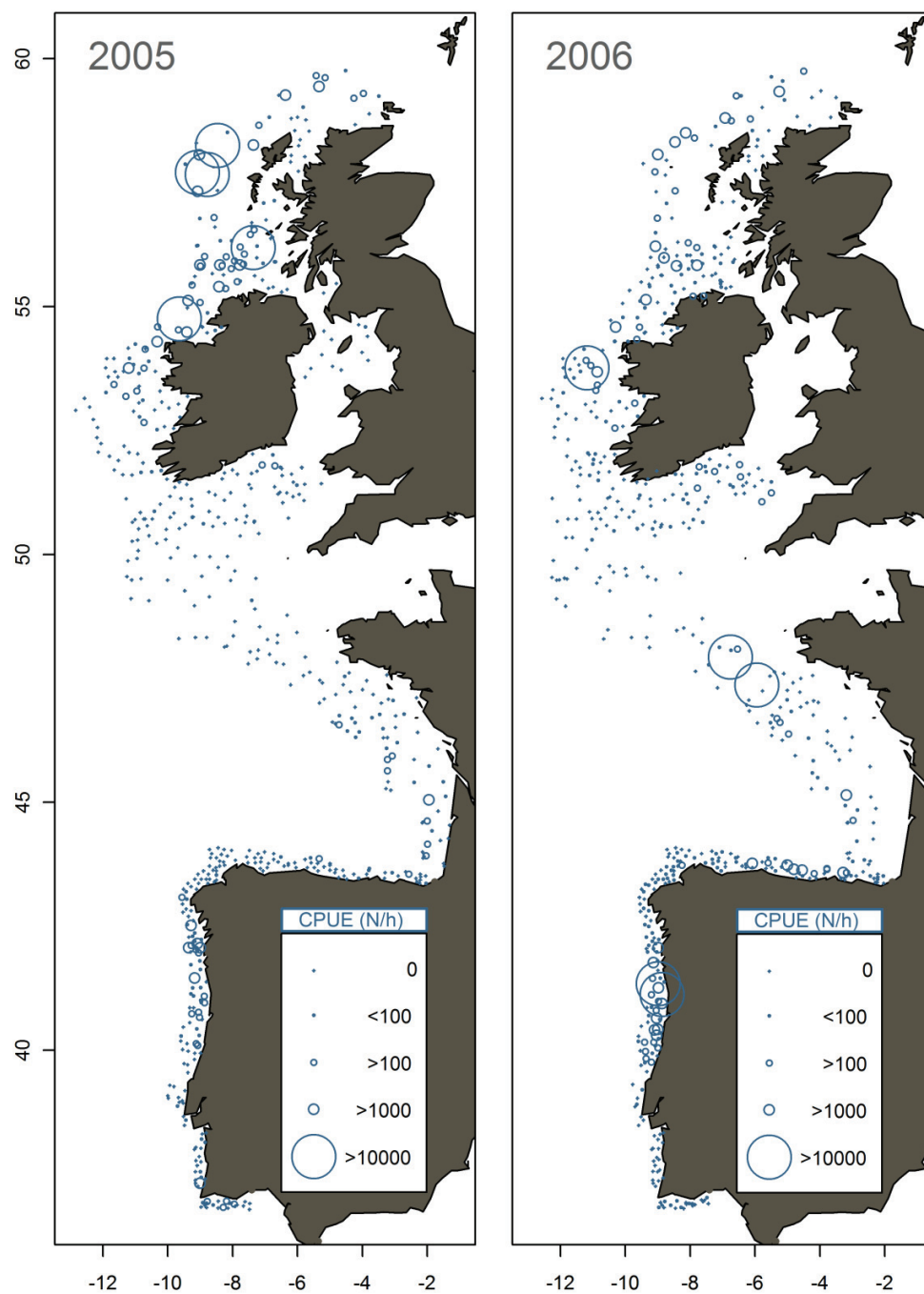


Figure 3. Spatial origin of recent strong year classes in the North East Atlantic. Catch Per Unit Effort (CPUE, numbers hour⁻¹) of juvenile mackerel at the age of zero in October-December 2005 and 2006 as reported to ICES WGWIDE.

Lumping and splitting

It could be argued that Atlantic mackerel meet the criteria for the strict definition of the metapopulation concept, sensu [16]. The criterion of more than one life-cycle pattern is clearly met by the isolation and differences across the Atlantic. Extinction is, like I argued for herring and cod, theoretically possible e.g. on one side of the Atlantic Ocean.

Whether the life-cycle complexes on each side of the Atlantic Ocean can be broken further into multiple contingents is more unclear. The finding of natal homing in the NEA and a weak phenotypic difference in the NWA indicate some structuring. However the North Sea component, previously thought to be the most distinct component in the NEA, was found to mix into spawning areas west of the British is. Furthermore, a recent strong year class from west of Scotland now appear to have spread to all spawning areas. Such weak structuring and substantial mixing is in accordance with the lack of solid genetic differences. On this basis, I suggest that the mackerel population in the NEA is better described as a dynamic cline, rather than connected entities. Hydrography and mackerel behavior may then affect the steepness of the gradient at various locations within the cline as these features vary for each generation. The classic treatment of the NEA mackerel as consisting of three isolated contingents (spawning components) is therefore unsupported and I find it likely that continued thinking along the classic lines may prevent progress towards improved understanding of mackerel in the NEA. More complex models are needed that can simulate dynamic levels of homing and straying across the entire spawning area and season – a more realistic model of life-cycle pattern diversity in the NEA. Under the assumption that mackerel in the NWA are similarly structured, then it is questionable how sensible it is to use the term “metapopulation” for Atlantic mackerel. It is not a “*population of local populations*” as Atlantic herring. I will therefore avoid using this term for Atlantic mackerel, based on the limited existing knowledge about Atlantic mackerel population structures.

Conservation of genetic and behavioral biodiversity is fundamental for sustainability. Optimal management yielding the maximum sustainable yield in an ecosystem management regime is likely to be compromised if the portfolio effect of diversity is reduced through generalized management [57]. This should also be of concern when managing mackerel fisheries, as some parts of the may be overexploited. However, the mackerel seems less prone to unbalanced exploitation than many other commercial species.

With this view on the mackerel population in the NEA, I revisit the largest known spatial changes in the history of Atlantic mackerel.

The historic collapse in the North Sea

The most dramatic change observed by mackerel scientists was the collapse in the North Sea in the 1970s [2]. Mackerel were highly abundant in the North Sea in the 1950s and 1960s. Larvae surveys showed that the spawning intensity varied greatly from year to year, but was generally on a very high level [2]. In the same decades, commercial landings of mackerel in the North Sea increased from < 50 to 50-100 kt, as the traditional mackerel fisheries with line and drift nets were supplemented by a Dutch trawl fishery [31,47]. In the late 1960s commercial fishermen on board Norwegian purse seiners realized that mackerel had very low target strength (acoustic reflectivity), which meant that the schools they could observe with the newly developed sonars actually represented a very large resource [58]. This discovery led to a targeted fishery utilising novel techniques such as power blocks and single-vessel purse seining. Landings consequently increased rapidly to peak at approximately 900 kt in 1967 (Figure 4) [31,48]. This is, even in 2011, unparalleled in numbers because the catch consisted of a high proportion of juveniles that were landed for industrial reduction [59,60]. The massive landings were followed by a collapse in the 1970s [48]. It was therefore concluded that the fishing pressure was too high and had caused the collapse [31,48]. From 1970 the Norwegian commercial fishery became regulated with quotas and later on with a minimum landing size. However the relatively high fishing pressure continued in the 1970s, supplemented by a new large pelagic trawl fishery that developed in the Celtic Sea e.g. off Cornwall where juveniles also constituted a significant part of the landings [61,62]. Despite subsequent regulations, designed specifically to protect the North Sea “component”, mackerel spawning never rebuilt to pre-collapse levels. In the last decade the spawning biomass has been 150-230 kt [1], which is significantly lower than before 1970 [2]. It is currently unknown why spawning in the North Sea has not rebuilt to former levels [2]. Outside the spawning season, millions of tonnes of mackerel started to spend autumn and winter in the Northern North Sea in the 1990s [3].

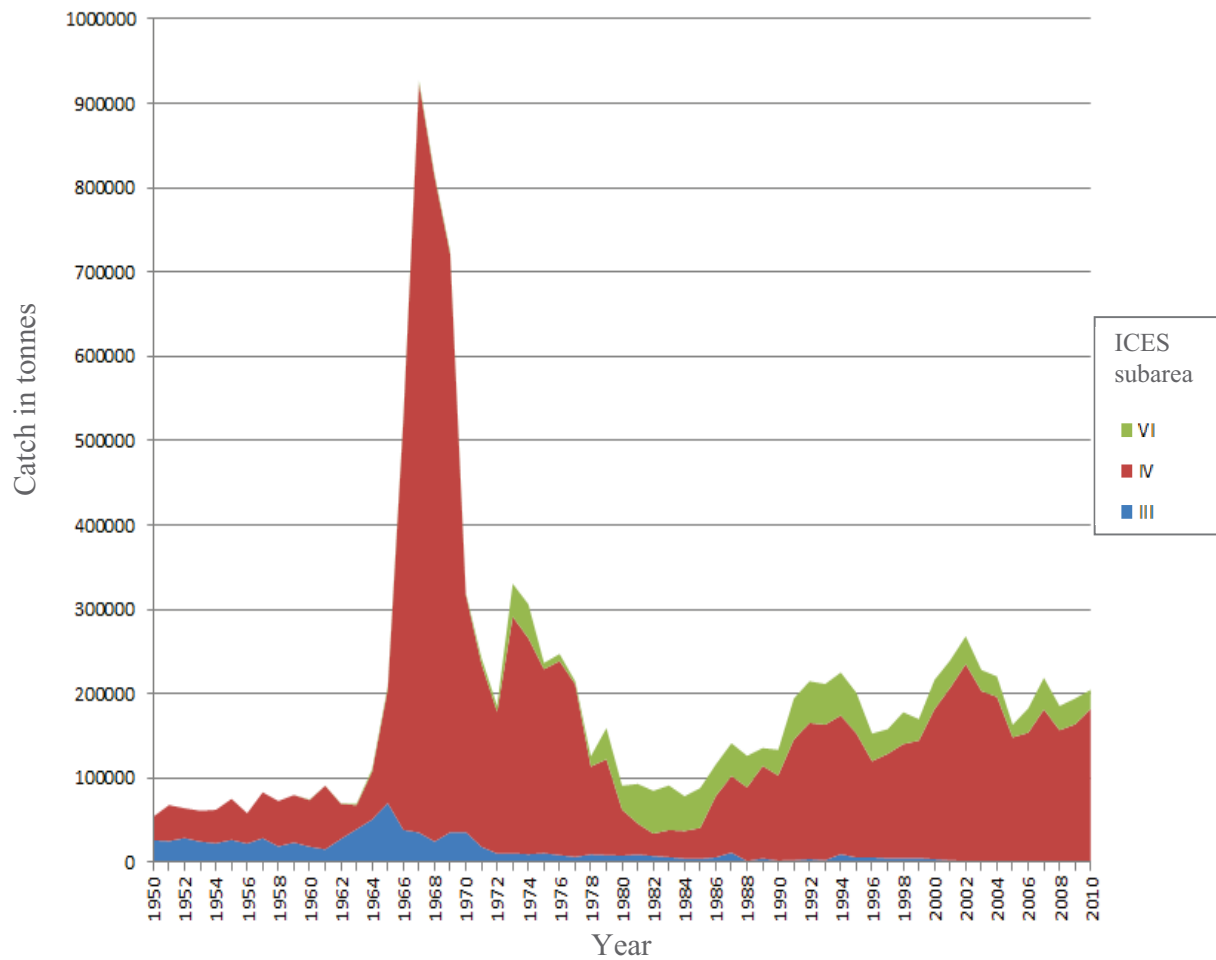


Figure 4. Commercial landings of mackerel in the North Sea (ICES subarea IV), Kattegat-Skagerrak (III) and West of Scotland (VI). Data from 1945-1949 from [47]. Data from 1950-2010 from [63].

The novel understanding of mackerel's spatiotemporal spawning distribution, as a result of the interplay between conservative repeated behaviour and dynamic responses to the environment, leads me to investigate alternative or additional explanations of the collapse in the North Sea. Rates of mixing and homing are not available; it is therefore impossible to build a quantitative population model of mackerel spawning biomass for any given area. However, a conceptual model based on the reviewed population processes can be used to interpret the historic developments. Such a conceptual population model of spawner biomass in the North Sea is shown in Figure 5. The model includes local recruitment with a tendency for homing. The homing can then be interrupted by other stimuli that lead the mackerel to other areas (straying).

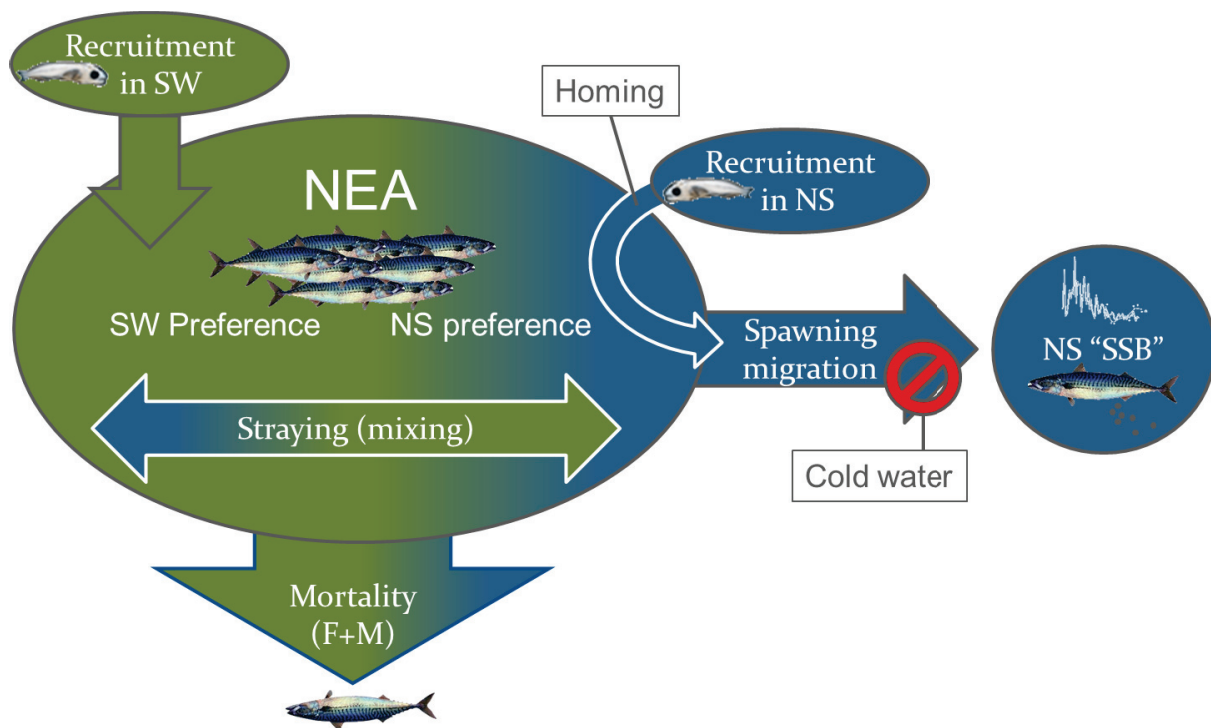


Figure 5. Conceptual model of spawning biomass (SSB) in the North Sea (NS) and areas further South-West (SW). Mortality can be due to fisheries (F) or natural causes (M) such as predation and disease.

Following environmental factors are considered:

- Temperature effects on the first part of the spawning migration during autumn and winter.
- Temperature effects on the last part of the spawning migration during spring.
- Zooplankton (food) during spawning
- Wind induced turbulence during spawning

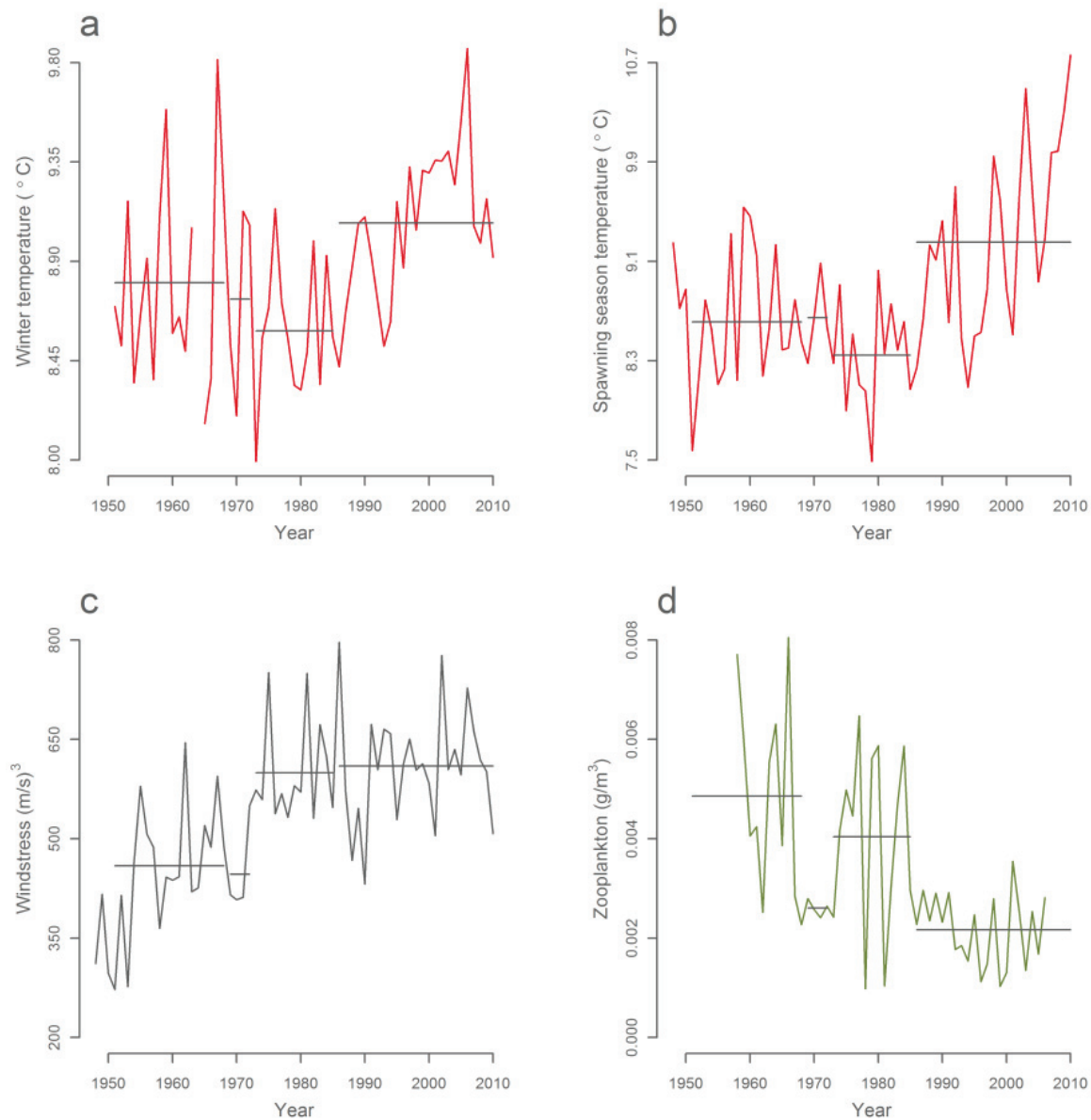


Figure 6. Time series of the four environmental variables that are known to affect spatiotemporal mackerel population dynamics and/or spawning in the North Sea. Horizontal lines show average over multiple years. (a) Sea temperature in autumn-winter (November-January). (b) Sea surface temperature in the early spawning season April-June. (c) Wind induced turbulence in the early spawning season May-June. (d) Mean zooplankton concentration in CPR samples during spawning in June (g/m³). Data sources and calculations are documented in appendix I.

Temperature effects on the first part of the spawning migration during autumn and winter

Winter temperature in the shelf edge current where mackerel overwinter affects the distribution prior to the spawning migration with a possible knock-on effect into the spawning season [3]. When NEA mackerel return from the feeding areas on the European shelf and in the Nordic Seas in late summer, they aggregate along the continental shelf edge west of the British Isles and up to the North Sea, where they stay throughout autumn and early winter and are targeted by commercial trawlers and purse seiners [1,3]. Later in winter the commercial fleets and fisheries independent bottom trawl surveys finds the mackerel further towards the southwest. The path of the migration, as suggested by the location of commercial and survey catches, coincides with the location of the relatively warm high-saline eastern Atlantic water flowing north-eastwards on and along the continental shelf edge, flanked by cooler water masses. The timing of the south-westwards migration is related to the long term temperature fluctuations of this current, most likely because the mackerel population is forced to seek warmer waters upstream as the current cools through winter. Mackerel was thus found further south-west during the relatively cold winters in the late 1970s and early 1980s, than in the 1990s and early 2000s (Figure 6a) [3]. Expansion of the temperature time series further back in time to the 1950s and 1960s revealed that this period was warmer than during the subsequent North Sea contingent collapse (Figure 6a). If temperature had similar effects on the overwintering distribution of the mackerel in those decades, as it had on the whole main NEA population in recent decades. Then the effect of cooling might have added to the reduction in spawning in the North Sea by moving mackerel, with an affinity for spawning in the North Sea, away from this area prior to spawning. Spatially disaggregated catch and survey data, as used by Jansen, Cambell et al. (Submitted) for analysing winter distributions from 1977-2010, were not available from 1950-1976. Literature was therefore reviewed to seek for descriptions of winter distributions that could support or reject the notion of a winter-temperature effect on the North Sea collapse. Two sources were found to be informative: Descriptions of the Norwegian purse seine fishery and fractions of 1969 year class in the commercial catches to the north west of Scotland:

- i) On the commercial winter fishery in the Norwegian Trench (inside the North Sea), Hamre (1980) wrote that it *“fluctuated considerably, owing to varying availability of the schools to the purse seiners. The mackerel were distributed in deeper water layers during winter, often below the range of the purse net, in order to avoid the winter-cooled surface layers. The winter fishery was therefore of minor importance to the purse-seine fleet”*.
- ii) Age distributions of the mackerel caught in November 1976, 1978 and 1979 to the north-west of Scotland (outside the North Sea) showed relatively large fractions of mackerel from the 1969 year class – an indicator of North Sea origin (Figure 2b).

The described avoidance of cool surface waters in the north-eastern North Sea fits the observations in the 1990s, where mackerel schools were found to concentrate in the core of relatively warm water flowing into the North Sea along the western edge of the Norwegian trench [64]. Hamre (1980) furthermore describes the varying availability of mackerel during winter inside the North Sea. This could be explained by a westwards emigration driven by cooling events. Indeed, the data from Walsh (1981) show that mackerel of North Sea origin was observed outside the North Sea in the late 1970s where the shelf edge current was relatively cold (Figure 6a).

The information from the literature, therefore supports, rather than rejects that distribution of mackerel, with an affinity for spawning in the North Sea, was affected by winter temperatures in the shelf edge current. This suggests a tendency for more mackerel during winter in the Northern North Sea in the 1950-1960s than during the subsequent decline in the 1970s. This environmentally driven change in winter distribution that appeared simultaneously with the collapse, pushed mackerel away from the North Sea prior to spawning.

Temperature effects on the last part of the spawning migration during spring

Spawning migration into the North Sea varies considerably in strength and timing [46,56]. During the decades up to the collapse, spawning in the North Sea was highly correlated with temperature in the surface waters of the North Sea bound currents. In the warm years, mackerel spawning was intensified in the North Sea and slightly reduced in the Celtic Sea, indicating that temperature affected mackerel's choice of spawning area [46]. It is therefore noteworthy that temperature in spring and early summer developed similarly to winter temperature, with cooling during the collapse in the 1970s and a warming during recent decades (Figure 6b). The link between temperature, during the last part of the spawning migration, and spawning suggests that the unfavourable cooling of the North Sea in the 1970s could have changed the spawning distribution, leading to a reduction of spawning in the North Sea.

Food and turbulence

Wind induced turbulence probably affects the suitability of spawning sites as it has been found to be negatively correlated with recruitment [65,66]. Turbulent mixing may disrupt food aggregations and the vertical distribution of eggs, larvae and juveniles, but the actual mechanisms behind the link between turbulence and recruitment remains unknown [65]. Zooplankton is important as food for both the adult and larvae [6]. It is therefore possible that turbulence and zooplankton concentrations affect spawning distribution of NEA mackerel through several processes.

Since the adult mackerel feeds through the spawning season [67,68], spawning mackerel is likely to be attracted to areas with high concentrations of zooplankton. Insufficient zooplankton concentrations (and high turbulence) in the North Sea may therefore reduce the spawning migration into the North Sea.

On the longer term, increased recruitment due to good feeding opportunities and/or low levels of turbulence would increase the numbers of mackerel with an affinity for spawning in the North

Sea, due to their natal homing behaviour. This would have effect on the spawner biomass and spawning intensity after 2-3 years, when the recruits mature.

Both zooplankton and wind changed in unfavourable directions during the collapse (Figure 6cd), it is therefore possible that this has added to the other negative changes in this period, through any of the suggested pathways.

The drivers of the collapse

The traditional explanation of the historic development of spawning in the North Sea seems to have overlooked a range of unfavourable environmental changes that might have added to the problems caused by the high fishing pressure. Quantifying and ranking the importance of each effect and their interactions is currently impossible, because insufficient data are available for a full quantitative model of all the involved processes. However it is possible to provide a holistic view of the available information about the key variables.

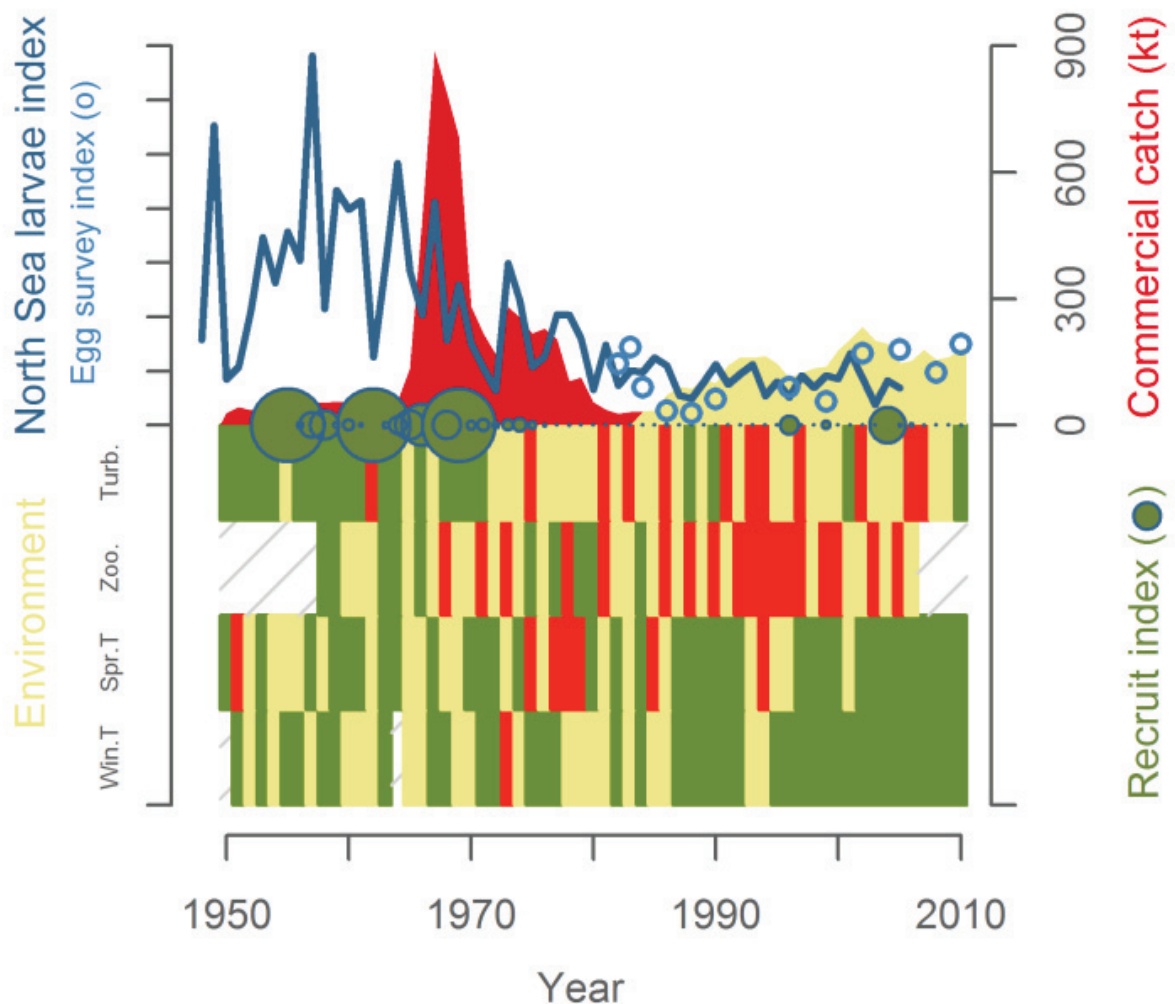


Figure 7. Summary plot combining information on the development of the North Sea contingent SSB (proxied by the larvae index (blue line) and egg index (blue circles)) with potential causal variables: Upper half: Commercial catch (red: North Sea (area 4), beige: west of the British Isles (area 6a)). Mid: Recruitment index (green circles). Lower half: 4 variables as traffic light plots: Winter temperature (Win T), Spring temperature (Spr T), Zooplankton concentration (Zoo) and wind induced turbulence (Turb). Traffic light colors indicate that annual values are either below the minimum (red), below the mean (beige) or above the mean (green) of the period of high mackerel abundance (1955-1967). Missing information is indicated by grey stripes. Data sources described in Appendix I.

The summary plot (Figure 7) shows the larval index as a proxy for North Sea spawner biomass, overlaid with information on the environment, recruitment and commercial catch. The plot illustrates how the period before the collapse is characterized by favorable or intermediate environmental conditions, good recruitment and very low fishing mortality. Then, in the late 1960s landings increase radically, environmental conditions change in unfavorable directions and recruitment ceases after the last good year class in 1969. The first two negative effects, overfishing and poorer feeding conditions, corresponds to the radical drop in spawning in 1970-1972. After an uncertain short rebuilding in 1972-1974 possibly related to good recruitment from 1969-1971 year classes [69], spawning in the North Sea as well as in the Celtic sea continued to decrease [70]. Through the 1970s substantial cooling was observed. The cool winters (Figure 6a) most likely forced mackerel away from the North Sea and the cool springs (Figure 6b) likely reduced and delayed the spawning migration into the North Sea. The increase in zooplankton concentration from around 1975 to the early 1980s (Figure 6d), did apparently not counter the combined effects of low temperature, lack of recruitment and continued fishing, as spawning in the North Sea continued to decrease. Then, large year classes in 1979, 1980 and especially in 1981 and 1984 originating from the west increased the population in the NEA [1]. However, no substantial straying effect seemed to support spawning in the North Sea. From the late 1980's temperatures increased to a level that in most years, matched or exceeded the early decades. But, at the same time zooplankton concentrations had decreased to the lowest level in the time series and turbulence remained high. These conditions likely kept recruitment and spawning in the North Sea on very low levels up until the early 2000's, where an increase in recruitment has been observed, while spawning remains on a relatively low level. Egg survey data suggests a slight increase in the last decade, but the larvae index is too uncertain in the latter decades to confirm this development [2].

The notorious “collapse of the North Sea component” thus seems to be a result of interactions between a high fishing pressure and environmental conditions acting to reduce recruitment and prevent spawning migration into the area.

Several similar cases of historic stock collapses caused by interactions between fishing and environment have been reported for other species, such as cod in the North West Atlantic [71] and the Baltic Sea [72].

The previously unexplained lack of rebuilding of spawning in the North Sea seems related to two environmental factors that have remained unfavorable, namely wind induced turbulence and zooplankton concentration (especially of the larger Calanoid copepods such as *Calanus Sp.*). Furthermore, the large commercial autumn-winter fishery in the North Sea and west of Hebrides continue to land unknown quantities of mackerel with an affinity for spawning in the North Sea. Assuming that mackerel, with an affinity to spawn in the North Sea, are among the last to leave the Northern North Sea and migrate along the continental shelf edge to the West of the British Isles. Then these mackerel have been exploited in recent years, such as in 2009 where parts of

the fishing fleet were restricted to fish up their very large quota in the Northern North Sea even though most mackerel had migrated west, due to decreasing temperatures [3].

Outlook for the North Sea

It is impossible to forecast fish population abundance more than a few years ahead due to the difficulties in predicting recruitment. This is also the case for mackerel [1]. However, some reflections on the possibilities for a rebuilding of the North Sea contingent seems possible in the context of the link between fishing mortality, environment, mackerel abundance and recruitment. Here, I address irreversible consequences of the collapse and future prospects for environmental conditions that may support life cycle closure for massive spawning in the North Sea.

The novel understanding of the population structure and collapse pave the way for discussing whether the collapse might have caused irreversible losses. As stated above, I assume some tendency for natal homing throughout the NEA. An average mackerel from the North Sea thus separates from an average mackerel from the western area, but how? If there should be a genetically based preference for homing to a certain area or environment, then it is not stronger than it can be overruled as seen by massive straying in the 2005 year class. The substantial high-frequency switching between spawning in the North Sea and further west, occurred before the collapse [46]. It is therefore likely that the genes from the mackerel that tended to spawn in the North Sea before the collapse were represented to a fair degree in the mackerel that tended to spawn further southwest. As a consequence of this, I suggest that the collapse in the North Sea may have changed some gene frequencies in the NEA, but not led to a distinct extinction of specific genes.

In the case that natal homing is based on learned recognition of certain environmental cues experienced during the first year, like for salmon [22], then the high mortality of the collapse and subsequent poor local recruitment have led to a significant behavioral loss. A behavioral loss of this type are not permanent and rebuilding could follow a reduction in mortality, substantial staying and if the environment still allows for life cycle closure. It can even be expected to happen faster than in cases where collapses result in the breakdown of socially transmitted traditions like for herring and cod [17]. There is no evidence of such a complex behavior of later entrainment of recruit (first time) spawners in mackerel, like it has been proposed for herring [17]. The tendency for homing shown by Jansen et al (Submitted) does not indicate this type of learning as the growth patterns that appeared in the first year disappeared in the second, before reappearing at spawning time throughout the adult life span. Furthermore, since the mackerel are not divided into relatively distinct contingents, like herring, I assume that this behavior is of minor importance or not existing.

Rebuilding is therefore not prevented by permanent historic losses, but depends on straying, mortality and environment.

The environmental conditions that have remained unfavorable since the collapse are zooplankton biomass and wind induced turbulence.

Confidence in predictions of wind speeds in the future is low. Several model studies have suggested increased average and/or extreme wind speeds in Europe, but some studies point in the opposite direction [73].

The long-term reduction in zooplankton biomass was mostly due to a reduction of larger copepods observed by CPR sampling— especially *Calanus finmarchicus* in the Northern North Sea. This is in accordance with previously published analysis of the same data set [74,75]. Abundance dynamics of *C. finmarchicus* in the North Sea in spring is driven by a combination of wind patterns and the volume of cold bottom water in the Faroe-Shetland Channel. In the winter, at depths greater than 600 m, the bottom water flowing south from the Norwegian Sea basin contains large numbers (up to 650 m⁻³) of hibernating *C. finmarchicus* [75]. In spring these copepods ascend to surface waters where advection transport parts of the population into the North Sea [75]. The bottom water in the Norwegian Sea is formed at high latitudes in the Greenland Sea by a process of cooling at the sea surface and sinking. Since the 1960s the intensity of this process has been decreasing due to warming and increasing freshwater inputs from Arctic rivers and ice melt [76]. The further transport into the North Sea appears to depend on wind strength and direction, factors that also changed in an unfavorable direction [75]. The additive combination of these physical changes is the likely reasons for the decrease in spring abundance of *C. finmarchicus* in the North Sea [75]. *C. finmarchicus* have furthermore been observed to seek the cooler waters below the thermocline when the surface waters become too hot [77]. This is also below the CPR sampling depths of approximately 7 m [78,79] and below the habitat of the smaller larvae [80,81]. However this latter effect is more pronounced in the warm months after the spawning. Anticipated future warming of the climate system has the potential to further weaken the thermohaline circulation by reducing surface water density in the areas where the North Atlantic Deep Water is formed through both high-latitude warming and enhanced poleward moisture transport in the atmosphere [82,83]. Assuming unchanged transport mechanisms of *C. finmarchicus* into the North Sea, this would not lead to any improvements in the possibilities for an increase in mackerel production in the North Sea in the years to come. However, mackerel is an opportunistic feeder and the larvae also seek other large species of zooplankton, so a major increase in mackerel spawning in the North Sea could happen if other preferred zooplankton species should increase in abundance.

While the spawning activity remains relatively low in the North Sea, it has recently increased in the main spawning areas of the NEA and expanded into new areas towards north-west [1].

The recent western and north-western expansion of the spawning area

In May-June 2010, spawning was observed further North-West of the main spawning areas than before (Figure 1c) [1]. It was the first time for the international egg survey to cover these areas

and therefore impossible to conclude whether the new observations reflected a recent expansion or merely an unknown part of the existing spawning area. Low egg concentrations ($<10 \text{ m}^{-2}$) were observed in most of the new area, except around Rockall and Hatton bank to the west of the standard survey area [9]. An exploratory survey in May 2002 found only a few eggs ($< 5 \text{ m}^{-2}$) around the Faroe, Rockall and Hatton banks [84] this was in contrast to the findings in the same month 8 years later. Historic records are few. While an exploratory egg survey covering Rockall bank in 1967 found some eggs [85], only 31 larvae were found in a new time series from CPR surveys showing that mackerel larvae were extremely rare in surface waters in 1948-2006 in these areas (Figure 9). The observations in 2010 thus reflected a recent expansion of the spawning area.

The reason for the recent expansion is unknown [1]. With a generally warming trend in the ocean and a NEAM population size larger than ever before in the ICES assessment time series from 1980 to 2010, ICES suggested temperature and density dependent expansion as potential causal effects together with food abundance and size distribution changes [1]. Wind induced turbulence is also a relevant factor to consider based in the North Sea analysis above and recruitment studies [65,66].

Wind induced turbulence during spawning in the new northwestern areas is stronger than it was in the North Sea in 1950-1969 (Figure 8ab). The new areas may therefore be less favorable for recruitment [65,66]. However, this needs to be considered together with data on zooplankton concentration and depth of the mixing layer – which was not a part of the present study.

The sea surface in the new spawning areas has been warming up in spring during the most recent years (Figure 8cd). In order to evaluate whether this change has improved the area as spawning habitat for mackerel, I compared the temperature observations with the temperature that were critical for the spawning migration into the North Sea in the high-abundance period (dashed line on Figure 8cd) [46]. Since the surface water in new western and north-western spawning areas recently became warmer than what appeared to be critical for the historic northern spawning migration, it can be concluded that with regards to temperature, these areas recently changed into a favourable mackerel spawning habitats.

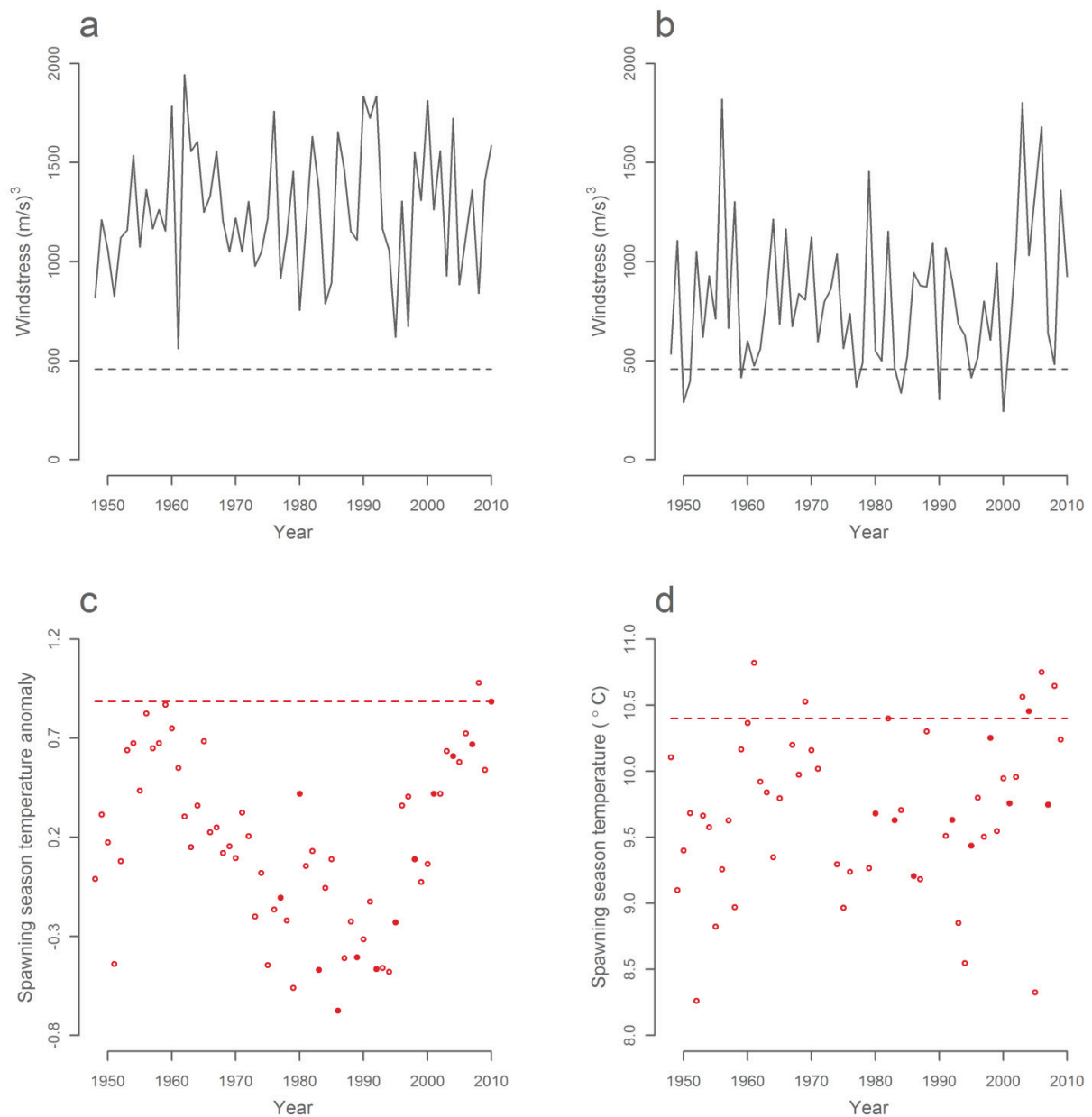


Figure 8. Average surface temperatures and wind induced turbulence during spawning on Rockall bank in May (ac), and Faroe bank in June (bd). Dashed line shows the average in June in the North Sea in 1950-1969. Filled circles indicate years with international western egg surveys. (Data: (ab) NOAA; (c) HadSST2; (d) ICES hydrographic database; See Appendix for detailed data descriptions).

The recent north-western expansion of the spawning area co-occurs with a western shift or expansion in the Nordic seas during the subsequent summer migration. This northern part of the summer distribution was viewed in a historic perspective by Astthorsson, Valdimarsson,

Gudmundsdottir, & Oskarsson (2012), who linked a century of mackerel observations in Icelandic waters with the Northern Atlantic temperature variability expressed in the Atlantic multidecadal oscillation (AMO). The link between temperature and mackerel observations, were interrupted by a striking lack of observations in the warm period of 1950-1963 (figure 7 in [86]). This period corresponds to the period where mackerel spawning in the North Sea was at its heights (Figure 7), suggesting some kind of interaction. The highly favourable conditions in the North Sea may have attracted most of the mackerel with northern affinities, leaving the area around Iceland with very little mackerel even though the temperature was adequate. While temperature is an obvious and important link between mackerel behaviour and large scale oceanographic features, too little is known about more complex roles of ocean circulation patterns; namely the zooplankton transport and production. Future effort should be directed into assessment of this effect on mackerel distribution and production.

Conclusion

Atlantic mackerel clearly displays isolated and different life-cycle patterns across the Atlantic Ocean. On each side, there seem to be a complex of spatiotemporal diversity, but it is not evident that they divide further into more closed life cycle patterns i.e. contingents. The tendency for natal homing within one of the traditional components show that mackerel exhibit the necessary behavioral element that act towards closure of spatiotemporal life cycle patterns on a more localized scale. However, no method has successfully been able to unequivocally identify the origin of spawning mackerel from any of the traditional spawning components. While most studies were found inconclusive, a weak phenotypic difference in the NWA indicated some structuring. On the other hand, the North Sea component, previously thought to be the most distinct component in the NEA, was found to mix into other spawning areas. Furthermore, a recent strong year class from West of Scotland now appears to have spread to other spawning areas. Such weak structuring and substantial mixing is in accordance with the lack of solid genetic differences. On this basis, I suggest that the mackerel population in the NEA is better described as a dynamic cline, rather than connected entities. Hydrography and mackerel behavior may then affect the steepness of the gradient at various locations within the cline as these features vary for each generation. As I did not find sufficient support for the three traditional contingents (spawning components), I find it likely that continued thinking along the classic lines may prevent progress towards improved understanding of mackerel in the NEA. More complex models are needed; models that incorporate dynamic levels of homing and straying across the entire spawning area and season, thus providing a more realistic simulation of the life-cycle diversity in the NEA. However, such a model would need to be parameterized with data that are currently not available. Future effort should therefore be directed at monitoring techniques that can provide the needed rates of mixing and migration. Tagging and natural tracers (e.g. chemical, demographic, growth or parasites) have the potential to provide such data for mackerel as they

have done for other species. These monitoring techniques should therefore be developed, standardized and implemented on a scale large enough to cover the mackerel life cycle.

A simple outline of this population model was used to investigate the most dramatic change in mackerel history, namely the collapse of the mackerel in the North Sea in the 1970s. I found that the traditional explanation of the collapse seems to have overlooked a range of unfavourable environmental changes that likely added to the effect of high fishing pressure. These parameters were:

- Temperature effects on the first part of the spawning migration during autumn and winter.
The information from the literature, supported, rather than rejected that the distribution of mackerel, with an affinity for spawning in the North Sea, was affected by decreasing winter temperatures in the shelf edge current. This environmentally driven change in winter distribution appeared simultaneously with the collapse, pushing mackerel away from the North Sea prior to spawning.
- Temperature effects on the last part of the spawning migration during spring.
The link between temperature and spawning migration in late spring and early summer, indicate that the unfavourable cooling of the North Sea in the 1970s changed the spawning distribution away from the the North Sea.
- Zooplankton (food) and wind induced turbulence during spawning.
Both zooplankton and wind changed in unfavourable directions during the collapse, it is therefore possible that this has added to the other negative changes in this period, through effects on spawning migration and/or recruitment.

I did not find indications for any irreversible genetic or behavioral loss caused by the collapse. The previously unexplained lack of rebuilding of spawning in the North Sea consequently seemed related to two environmental factors that have remained unfavorable, namely wind induced turbulence and zooplankton concentration (especially of the larger Calanoid copepods such as *Calanus Sp.*). Furthermore, the large commercial autumn-winter fishery in the Northern North Sea continues to land unknown quantities of mackerel with an affinity for spawning in the North Sea. Rebuilding of spawning, to a pre-collapse level, therefore seems possible under favorable environmental conditions and sufficient conservation of mackerel with an affinity for spawning in the North Sea.

While the spawning activity remains relatively low in the North Sea, it has recently increased in the main spawning areas of the NEA and expanded into new areas towards north-west. Since the surface water in the new north-western area recently became warmer than what appeared to be critical for the historic northern spawning migration into the North Sea, it can be concluded that with regards to temperature, these areas have become favourable as a mackerel spawning habitats.

While temperature clearly is important for mackerel, too little is known about more complex roles of ocean circulation patterns; namely the zooplankton transport and production. Future effort should be directed into assessment of this effect on mackerel distribution and production.

Conservation of genetic and behavioral biodiversity is fundamental for sustainability. Optimal management yielding the maximum sustainable yield in an ecosystem management regime is likely to be compromised if the portfolio effect of diversity is reduced through generalized management [57]. This should also be of concern when managing mackerel fisheries, as some parts of the population may be overexploited. However, the mackerel seems less prone to unbalanced exploitation than many other commercial species.

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Appendix I - Materials and methods

Environmental variables

Four temperature time series were compiled:

1. A yearly average spring sea surface temperature (Spr T) was selected to reflect temperature conditions prior to and during spawning in North Sea surface waters. Yearly average spring sea surface temperature were estimated as the average of monthly values in April-June in $2^{\circ} \times 4^{\circ}$ rectangles and for the area $56-62^{\circ}\text{N}$, $0-4^{\circ}\text{E}$. Observations originated from depths of $<10\text{m}$ from CTD/bottles/underway/pump/moorings and were obtained from *ICES hydrographic database* [87].
2. The temperature in the continental shelf edge current, that flow along the western edge of the Norwegian trench (Figure 1-2 in [3]) was selected to represent the conditions experienced by mackerel through winter (Win T). Mackerel distribution during winter is related to this temperature, possibly with a propagating effect on spawning [3]. Details of this modelled temperature time series have previously been published [3]. Here I followed the same approach and extended the time series back to 1951 with available temperature profiles from CTD stations and bottle sampling between November, obtained from the ICES hydrographic database [87].
3. Two time series of yearly sea surface temperatures were compiled to reflect the conditions during the spawning season in the new north-western spawning areas; one for the Rockall bank and one for the Faroe bank:
 - a. Yearly sea surface temperatures around the Faroe bank in 1948-2010 were estimated as the average of monthly SST in May in the area $60-62^{\circ}\text{N}$, $7-10^{\circ}\text{W}$ (selection of area and months was based on egg survey results from the 2010 survey [1] and availability of observations). Observations originated from depths of $<10\text{m}$ from CTD/bottles/underway/pump/moorings and were obtained from *ICES hydrographic database* [87].
 - b. Yearly sea surface temperature anomalies around the Rockall bank in 1948-2010 were estimated from a coarser modeled and validated dataset of sea surface temperatures (SST) obtained from the Hadley Centre SST data set (HadSST2) [88], by averaging over a larger geographical box covering the area ($55^{\circ}\text{N}-60^{\circ}\text{N}$, $15-20^{\circ}\text{W}$) in May. Selection of area and months was based on egg survey results from the 2010 survey [1]. In order to compare the time series of anomalies with the absolute value of 10.4°C that was found critical for spawning migration into the North Sea, I matched the 2010 anomaly with the mean temperature (10.3°C) measured at 5 m on positions where eggs were found in the area during the international egg survey in 26-29 April 2010.

Turbulence may affect the suitability of spawning sites and has been found to correlate with recruitment [65]. Wind stress (= cube wind speed) data set “esrlIcoads2ge” was downloaded as gridded (2° lat x 2° lon) monthly averages from the NOAA ICOADS website (<http://coastwatch.pfeg.noaa.gov/erddap/griddap/esrlIcoads2ge.html>). Seasonal means were calculated for the spawning season and area in 1948-2010 in the North Sea (May-June, 50-60°N 4°W-8°E). For the new north-western spawning areas; Rockall bank (April-May, 54-58°N 13°W-17°W) and Faroe bank (May, 60-62°N 5°W-13°W), the selection of area and months was based on egg survey results from the 2010 survey [1] and availability of observations.

Zooplankton data from Continuous Plankton Recorder (CPR) surveys from 1958 to 1974 were obtained from the SAHFOS database as abundance by species by sample. Data from 1948-1957 were not available by species. Biomass by sample was calculated using the mean dry weight by species from [74]. Mean zooplankton density (g/m³) by year were calculated as a simple average of all samples in the North Sea (50-60°N 4°W-8°E) in the peak spawning season (June). Biomass was used instead of abundance because mackerel in all life stages are size selective feeders and prefer larger Calanoid copepods over smaller Cyclopoid copepods [89-93]. The CPR is known to under-sample in some situations. This mostly affects smaller species and was therefore ignored [74].

Recruitment data

Four time series of recruitment in the North Sea were used to identify strong year classes. 1) Catch rates of 4 year old mackerel in the 1955 – 1961 year classes in the Dutch trawl fishery assuming these were fully recruited to the fishery [47]. 2) Number of recruits of the year classes 1962 – 1970 from a landings and tagging based assessment [48]. 3) Catch rates of first winter juveniles from the international bottom trawl survey (IBTS) in the first quarter of 1968 - 1979 from [94]. 4) Catch rates of first winter juveniles in the first quarter of 1973 - 2010 from the ICES DATRAS database (<http://datras.ices.dk>). The four recruitment indices were thus not on the same absolute scales. In order to visualize the strong year classes within the same plot, I standardized the values in each data set to the mean of each time series. The last time series of catch rates were further downscaled by an arbitrary factor of 0.2.

Mackerel larvae from CRP survey

A new time series of mackerel larvae in the new northwestern spawning areas (Figure 9) are based on mackerel from Continuous Plankton Recorder (CPR) surveys. This unique time series does unfortunately not include the most recent years of expansion. Sampling and analysis details have been published in [2,95].

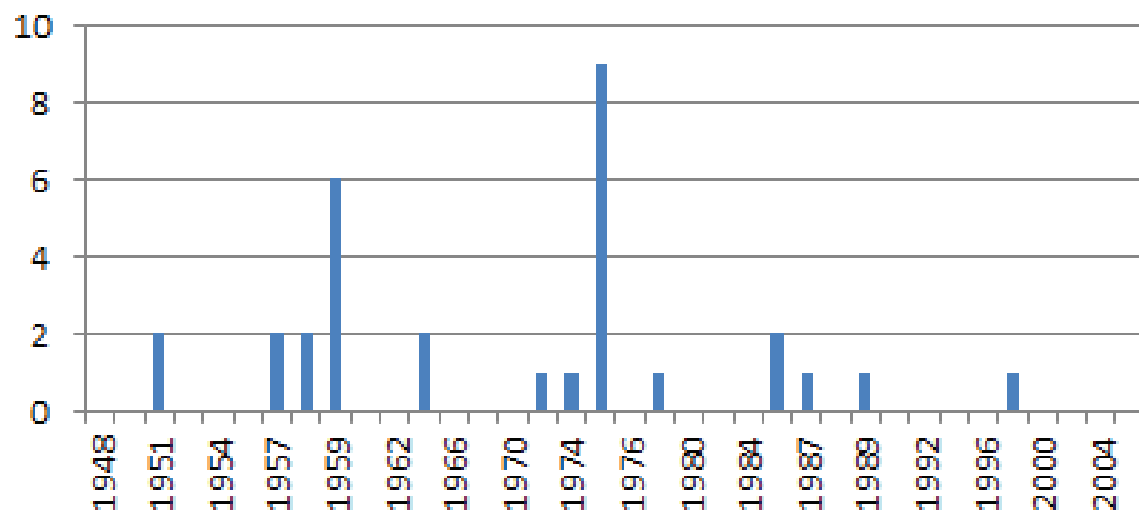


Figure 9. Mackerel larvae caught in CPR surveys northwest of the standard egg survey area (N.of 56°N, W.of 12°W or N.of 50.5°N, W.of 7.5°W)

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